The Great Lakes Entomologist

Volume 52
Numbers 1 & 2 - Spring/Summer 2019 *Numbers 1 & 2 - Spring/Summer 2019*
Article 1

September 2019

TGLE Vol. 52 Nos. 1 & 2 Full Issue

Vol. 52, Nos. 1 & 2 Spring/Summer 2019

THE GREAT LAKES ENTOMOLOGIST

PUBLISHED BY

THE MICHIGAN ENTOMOLOGICAL SOCIETY

THE MICHIGAN ENTOMOLOGICAL SOCIETY 2018–19

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Epeoloides pilosulus (Cresson) (Hymenoptera: Apidae) Rediscovered in Michigan, with Notes on the Distribution and Status of its *Macropis* Hosts

T.J. Wood[1,2*], M.F. Killewald[1,3], K.K. Graham[1], J. Gibbs[3] and R. Isaacs[1]

[1] Department of Entomology, Michigan State University, East Lansing, MI, 48824, USA

[2] Current affiliation: Laboratory of Zoology, University of Mons, 7000, Mons, Belgium

[3] Department of Entomology, University of Manitoba, 12 Dafoe Rd., Winnipeg, MB, R3T 2N2, Canada

*Corresponding author: (e-mail: thomasjames.wood@umons.ac.be)

Abstract

Epeoloides pilosulus (Cresson 1878) (Hymenoptera: Apidae) is one of the rarest bees in North America with only a handful of records since 1960. *Epeoloides pilosulus* is a brood parasite of *Macropis* bees, which until recently had not been collected in Michigan since 1944. Bee surveys in Midland County, Michigan have led to the rediscovery of *E. pilosulus* in this state – the first record in 74 years. Michigan becomes the fourth state where *E. pilosulus* has been rediscovered after Connecticut in 2006, New York in 2014 and Maine in 2016, and the sixth region in North America after Nova Scotia in 2002 and Alberta in 2010. State-wide bee surveys have also shown that the principal host, *Macropis nuda* (Provancher 1882), remains widespread in Michigan, and that *Macropis patellata* Patton 1880 is newly recorded for the state.

Key words: parasitic bee, oil bee, oligolege, bee surveys, *Lysimachia*

The status of wild bee species and populations has been the subject of a great deal of attention by the scientific community in recent years, with rapidly contracting distributions for bees such as *Bombus affinis* Cresson documented in the United States and Canada (Colla and Packer 2008; Cameron et al. 2011). Understanding population declines in wild bees outside of the genus *Bombus* has been more difficult, in part because many solitary bee species are rare in collections, either because they have small geographic ranges or because they are phenologically limited to a narrow flight period and require specialized collection effort in order to detect (Harrison et al. 2017). Indeed, in a study of the population trends of wild bees in the northeastern United States, 87 of the 438 species (19.9%) were represented by only 10 to 30 specimens over a 140-year period, making assessment of their historic and contemporary statuses challenging (Bartomeus et al. 2013).

One bee species that has been very infrequently recorded in North America is *Epeoloides pilosulus* (Cresson). *Epeoloides pilosulus* is a brood parasite of *Macropis* bees (Sheffield et al. 2004; Wagner and Ascher 2008), which are themselves specialists on *Lysimachia* species (Fig. 1A, Primulaceae), collecting pollen and floral oils exclusively from this genus (Michez and Patiny 2005). Floral oils are mixed with pollen provisions and used to waterproof the linings of the cell wall (Cane et al. 1983), allowing *Macropis* to nest in the damp soils favored by *Lysimachia* species (Fig. 1B). *Epeoloides pilosulus* is thus twice restricted; first by the limited suite of bee species that it parasitizes and second by the narrow ecological niche occupied by its hosts.

Epeoloides pilosulus is consequently very rarely collected. Most specimens in Michigan were collected in the early part of the 20th century with the last record made in 1944. This fits into the overall trend for *E. pilosulus*, as the species was not recorded in North America between 1960 and 2002 (but see Sheffield and Heron 2018), until it was rediscovered in Nova Scotia based on two male specimens collected in a pan trap (Sheffield et al. 2004). There have only been four additional contemporary records of *E. pilosulus* in North America since then, in Connecticut (2006, Wagner and Ascher 2008), Alberta (2010, Sheffield and Heron 2018), New York (2014, http://bugguide.net/node/view/954741), and Maine (2016, Dibble et al. 2017). In Michigan, *E. pilosulus* is known from four counties in the central and southern Lower Peninsula (Berrien, Midland, Van Buren, and Wayne).

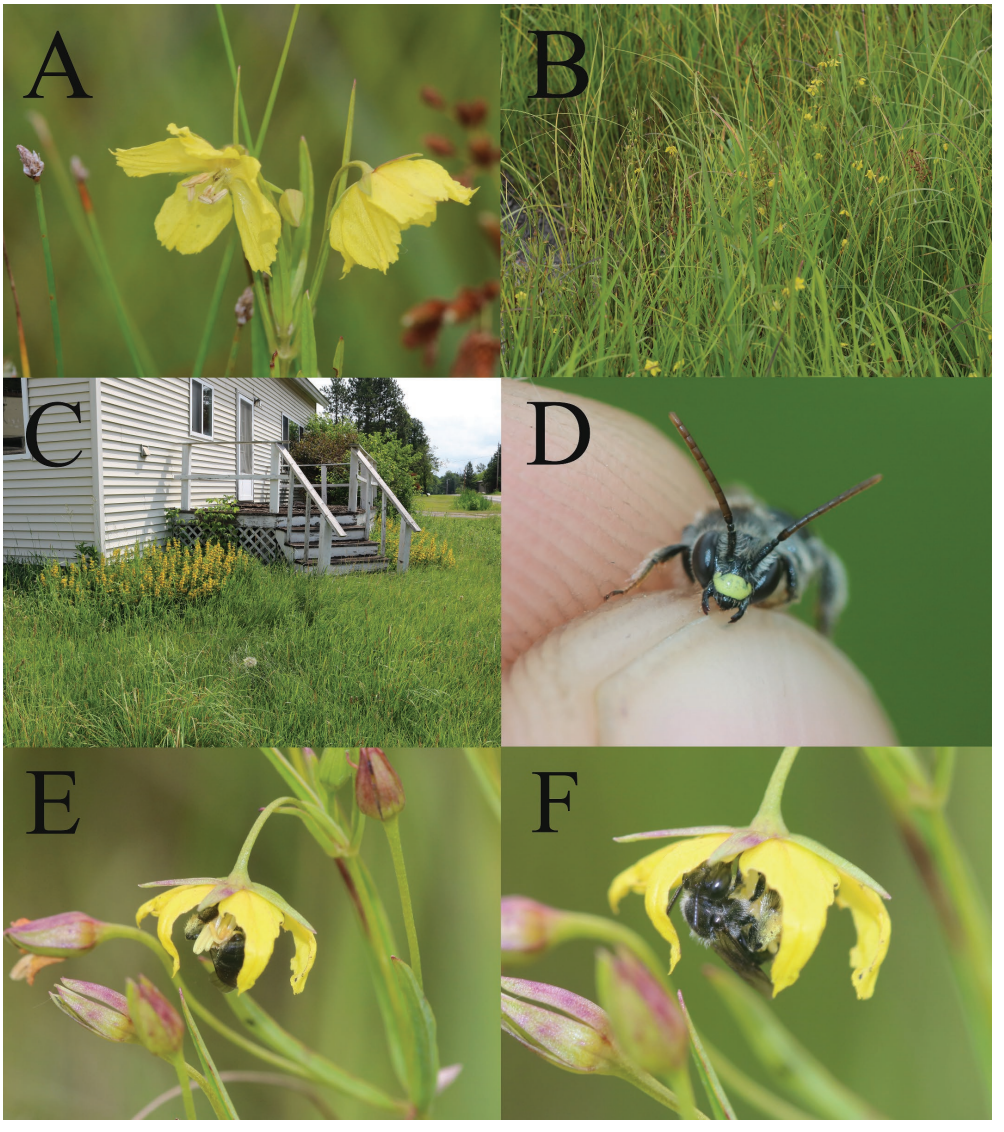

Figure 1. A. Fringed Loosestrife (*Lysimachia ciliata* L.) flower. B. *Lysimachia ciliata* in flower in damp prairie fen habitat at Ives Road Fen, Lenawee County. C. European Dotted Loosestrife (*Lysimachia punctata* L.) outside an abandoned house in Felch, Dickinson County. D-F. *Macropis nuda* (Provancher) individuals at Algonac State Park, St. Clair County. D. *Macropis nuda* male showing distinctive yellow facial maculations. E-F. *Macropis nuda* female collecting pollen from *L. ciliata*.

Only one species of *Macropis* has been recorded from Michigan – *Macropis nuda* (Provancher). *Macropis nuda* has a large range and is known from Canada, from British Columbia to Nova Scotia, and the United States, from Montana and Colorado to the New England states (Mitchell 1960; Michez and Patiny 2005; Sheffield and Heron 2018). However, like *E. pilosulus*, *M. nuda* appeared to have disappeared from Michigan, being last recorded in 1959 and not rediscovered until 2017 in Hillsdale County (Gibbs et al. 2017).

The aim of this paper is to report on the findings of recent bee faunal surveys across Michigan that include the rediscovery of *E. pilosulus* and have expanded our understanding of the status of *Macropis* species in the state.

Methods

As part of our Michigan bee survey we visited the Averill Preserve (43.6618, –84.3500; managed by Little Forks Conservancy) in Midland County every other week from mid-June to mid-September in 2017 and 2018. During each visit, we spent one cumulative hour sampling bees using aerial nets, and we recorded which plants bees were caught on. Surveys focused on open habitats, with surveyors searching all flowering plants within these areas. Similar sampling methods were used at seven other sites in Midland, Ingham, Shiawassee, Kalamazoo, and Livingston counties. All bees were pinned and labelled at Michigan State University, and then identified to species at the University of Manitoba (JG and Joel Gardner). During collection at the Averill Preserve, a specimen of *E. pilosulus* was captured (see Results). This material is deposited in the Albert J. Cook Arthropod Research Collection at Michigan State University.

The records of *Macropis* species for Michigan stated in this paper are based on the collections of the lead author as part of his efforts to survey wild bees in every county in Michigan. His material is deposited at the J.B. Wallis / R. E. Roughley Museum of Entomology, University of Manitoba. Historic records of *E. pilosulus* and *M. nuda* collections were taken from the most recent summary of the Michigan bee fauna (Gibbs et al. 2017).

Results

Epeoloides pilosulus (Cresson 1878)

Current records: *Midland Co.*: Midland, Averill Preserve, 43.6618, –84.3500, M. Killewald, 28 June 2018, 1♀, (BH_010955), *Lysimachia nummularia* L.

The specimen was collected as it was patrolling a small patch of *L. nummularia* flowers along a walkway.

Macropis (*Macropis*) *nuda* (Provancher 1882)

Current records: *Alcona Co.*: Black River, Black River Road x La Vigne Road, 44.815, –83.324, T.J. Wood, 15 July 2018, 1♀, *Apocynum androsaemifolium* L.; ***Alpena Co.*:** Mackinaw State Forest, Long Rapids Rd x Truax Creek, 45.116, –83.823, T.J. Wood, 15 July 2018, 1♂, 1♀, *Lysimachia ciliata* L.; ***Dickinson Co.*:** Foster City, Felch, 45.996, –87.825, T.J. Wood, 30 June 2018, 2♂, *Lysimachia punctata* L., Fig. 2C; ***Hillsdale Co.*:** Pittsford State Game Area, 41.866, –84.522, T.J. Wood, 8 July 2017, 1♂, *Apocynum cannabinum* L.; ***St. Clair Co.*:** Algonac State Park, 42.650, –82.531, T.J. Wood, 14 July 2018, 1♂, 1♀, *L. ciliata*, Fig. 1D–F; ***Tuscola Co.*:** Dayton, S Plain Road x James Road, 43.462, –83.268, T.J. Wood, 25 June 2018, 1♂, 1♀, *L. ciliata*.

Macropis nuda was not known from Alcona, Hillsdale, St. Clair and Tuscola counties prior to its discovery there in 2017–2018. The historic and contemporary distributions are shown in Fig. 2A.

Macropis (*Macropis*) *patellata* Patton 1880

Current records: *Lenawee Co.*: Ives Road Fen Preserve, 41.967, –83.945, T.J. Wood, 8 July 2018, 3♂, *L. ciliata*.

Males and females were abundant at an area of restored prairie fen in south-east Michigan with regenerating wetland vegetation (Fig. 2B). No females were collected as TJW believed at the time that these bees were *M. nuda*, and consequently did not collect any females in order to avoid depleting the population. It was not until they were inspected under the microscope that their true identity was determined.

Discussion

The rediscovery of *E. pilosulus* in Midland County suggests that the species has been present in Michigan continuously since it was first discovered over a century ago. Although *M. nuda* was not also found at the same site, the host and the parasite are often detected using different sampling techniques, with the parasite detected using bowl traps and the host using aerial netting in both Nova Scotia and Connecticut (Sheffield et al. 2004; Wagner and Ascher 2008). Contemporary records of *M. nuda* suggest that this species remains most common in the Saginaw Bay region of eastern Michigan (Fig. 2A).

All pollen foraging *M. nuda* females along with several males were collected from Fringed Loosestrife (*L. ciliata*). This is in common with other studies in eastern North America (Cane et al. 1983). Males were also collected patrolling around the introduced European Dotted Loosestrife (*L. punctata*) in Dickinson County (Fig. 1C), suggesting that it may also be visited by females of this species. In Europe, *L. punctata* is visited for pollen and oil by the native *M. fulvipes* (Fabricius) (Michez and Patiny 2005). In contrast, the European Creeping Jenny (*L. nummularia*) is not visited by *Macropis* species (Cane et al. 1983) as it does not produce oil. This may explain why *E. pilosulus* was found at the Averill Preserve site but *M. nuda* was not. Surveys

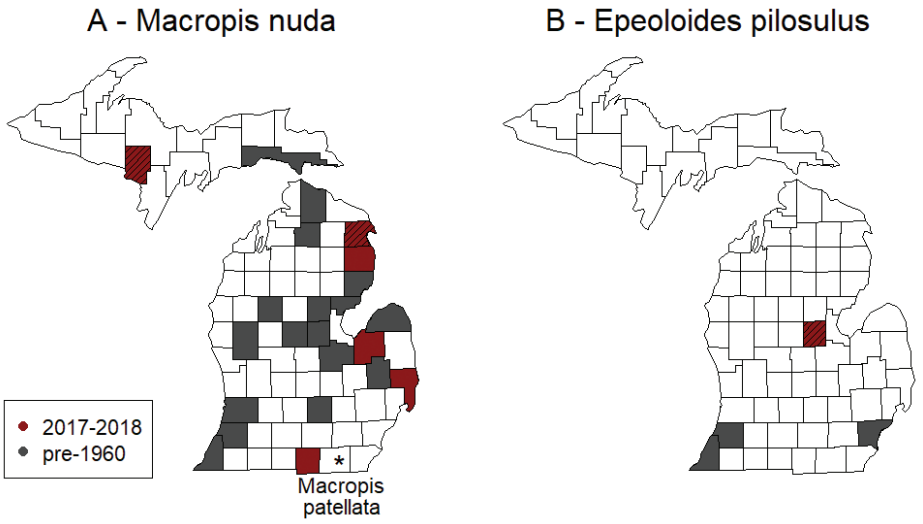

Figure 2. A. Distribution of *Macropis nuda* (Provancher) in Michigan at a county-level resolution. The single new record of *Macropis patellata* Patton is marked with an asterisk. B. Distribution of *Epeoloides pilosulus* (Cresson) in Michigan at a county-level resolution. Pre-1960 records are marked in gray and 2017–2018 records are marked in red. Hatching indicates records of the species in both time periods.

were restricted to dry, open areas, where no other *Lysimachia* species were present, although they may have been present in damp riverine areas nearby. Individual females of *M. nuda* collected on Indian Hemp (*A. cannabinum*) and Spreading Dogbane (*A. androsaemifolium*) showed no evidence of pollen collection and were visited solely for nectar. Though restricted to *Lysimachia* for pollen and floral oils, *Macropis* species have been recorded visiting many plant families for nectar (Pekkarinen et al. 2003; Michez and Patiny 2005), including *Apocynum* by *M. nuda* (Cane et al. 1983).

Macropis patellata is known to occur in the eastern United States from North Carolina north to Vermont and west to Iowa and Nebraska (Mitchell 1960; Michez and Patiny 2005; Ascher and Pickering 2018). Surprisingly, the species has never been recorded from Indiana or Ohio, so this record from south-eastern Michigan fills a distributional gap and suggests that, in addition to these two states, the species may also be present in southern Ontario. Most of the data used to determine the distribution of this bee are old, and the species was highlighted as potentially being of conservation concern due to a lack of recent records in the northeastern United States (Bartomeus et al. 2013). The two other *Macropis* species known from North America, *M. ciliata* Patton 1880 and *M. steironematis* Robertson 1891, have a similar distribution to *M. patellata*, being found in some Atlantic states and parts of the Midwest, but have not been recorded from Michigan, Indiana or Ohio (Michez and Patiny 2005; Ascher and Pickering 2018). Continued targeted searching may reveal the presence of one or both of these additional *Macropis* species in this region.

The rediscovery of *M. nuda* (Gibbs et al. 2017) and *E. pilosulus*, as well as the discovery of *M. patellata*, in Michigan highlights some potential consequences of low sampling effort for bees over long periods of time. These include a high likelihood of missing bees that have restricted geographical ranges or that exploit a narrow range of host plants, as well as the potential to consider a bee rare when it has instead been poorly sampled. The level of active sampling for bees in Michigan has, until very recently, been low in comparison with the historical baseline. The year of the most recent previous record for *M. nuda* (1959) coincides with the final collection period of R.R. Dreisbach, a prolific amateur entomologist who collected bees extensively across the whole state (Fischer 1965). *Macropis nuda* and *E. pilosulus* were almost certainly continuously present in Michigan for the last 60–70 years, and the absence of records for these species likely reflects low sampling effort rather than a genuine population decline. More regular and extensive sampling is needed to inform conservation efforts along with targeted searches to understand the

abundance and distribution of specialized species that have narrow ecological niches which make them difficult to detect. General bee surveys in North America are likely at an all-time high, but many species of conservation concern may best be studied with more focused efforts.

Acknowledgments

Survey work was funded by USDA NIFA grant 2017-68004-26323. Our thanks go to Gary Parsons for access to the insect collection at MSU, to The Little Forks Conservancy for allowing access to the Averill site, and to The Nature Conservancy for allowing access to the Ives Road Fen site.

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The Discovery of *Trissolcus japonicus* (Hymenoptera: Scelionidae) in Michigan

Benjamin J.M. Jarrett[1*], John Pote[1], Elijah Talamas[2], Larry Gut[1] and Marianna Szucs[1]

[1] Department of Entomology, Michigan State University, East Lansing, MI 48824

[2] Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Gainesville, FL 32608

[*]Corresponding author: (e-mail: bjarrett@msu.edu)

Abstract

The invasive brown marmorated stink bug, *Halyomorpha halys* (Stål) (Hemiptera: Pentatomidae), is a pest of growing economic importance in the United States, the control of which currently relies on pesticide applications. Biological control could provide sustainable and long-term control but classical biological control agents have not yet been approved at the federal level. Adventive populations of a potential biological control agent, the Samurai wasp, *Trissolcus japonicus* (Ashmead) (Hymenoptera: Scelionidae), have been found in the United States, first in Maryland in 2014, expanding its range west to Ohio by 2017. *Trissolcus japonicus* is a highly effective parasitoid of *H. halys* eggs, but its redistribution and augmentative releases are restricted to states where it has been detected in the wild. To assess the presence of *T. japonicus* in Michigan and attack rates on *H. halys* by native natural enemies we deployed 189 *H. halys* egg masses at ten sites in lower Michigan between May and October in 2018. In addition, we deployed 51 native stink bug egg masses at the same sites to evaluate potential non-target effects of *T. japonicus* in the field, which were shown to occur in laboratory studies. We found *T. japonicus* in a single *H. halys* egg mass, which constitutes the first record of this Asian parasitoid in Michigan. Native predators and parasitoids caused minimal mortality of *H. halys* eggs and we did not find evidence of non-target effects of *T. japonicus* on native stink bug species. These findings open the door to initiation of a classical biological control program using an efficient, coevolved parasitoid from the native range of *H. halys*.

Keywords: Samurai wasp, brown marmorated stink bug, BMSB, biological control, sentinel egg masses, *Halyomorpha halys*

Invasive insects can cause significant economic damage to crops, especially in large monocultures (Bradshaw et al. 2016), potentially because they exist in their invaded ranges without their coevolved natural enemies (Roy et al. 2011). The brown marmorated stink bug, *Halyomorpha halys* (Stål), is an invasive pentatomid pest that was first detected in the United States in 1996 (Hoebeke and Carter 2003). It is capable of feeding on over 200 host plants, including many species of agricultural importance and has caused significant economic damage in the mid-Atlantic region (Leskey et al. 2012, Leskey and Nielsen 2018). Control of *H. halys* currently relies on pesticide applications, largely due to the absence of alternative control strategies like biological control agents (Rice et al. 2014). Native natural enemies have very limited impact on *H. halys* populations, with egg parasitoids attacking usually < 5% of egg masses (Abram et al. 2017, Dieckhoff et al. 2017). Thus, repeated applications of broad-spectrum insecticides over the growing season are necessary to control this pest in cropping areas, but given the vast host range of *H. halys*, populations can always persist in natural areas and recolonize crops. Biological control can suppress *H. halys* numbers across the landscape but to date no effective natural enemies have been found in Michigan.

Two parasitoid species that attack *H. halys* in its native range have been under consideration for release as classical biological control agents since 2007, with one, *Trissolcus japonicus* (Ashmead), undergoing host range testing. *Trissolcus japonicus* was found to develop on at least seven native stink bug species in Oregon (Hedstrom et al. 2017) and 15 native species in Michigan (Botch and Delfosse 2018), which would likely prevent its approval for field release. Nevertheless, *T. japonicus* found its own way into the United States, most likely from parasitized *H. halys* egg masses (Talamas et al. 2015b). Adventive populations were initially detected in Maryland (Talamas et

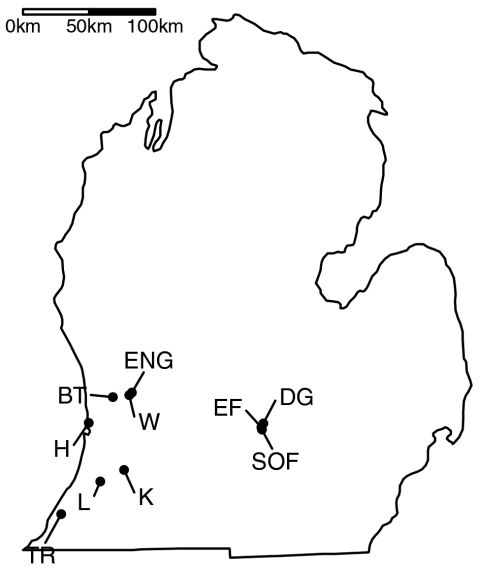

Figure 1: Map of sites where sentinel egg masses were deployed. Site codes are listed in Table 1. *Trissolcus japonicus* was captured at the MSU Student Organic Farm (SOF) in August 2018. *Trissolcus euschisti* was found at the orchard site ENG, and *T. brochymenae* was found at the mixed site W.

al. 2015b) and soon thereafter in neighboring states (Buffington et al. 2018). Based on the pattern of discovery, *T. japonicus* populations are gradually moving west and north, having been found in Pennsylvania and Ohio in 2017. Adventive populations have also been found in western Canada and Oregon, although these are presumably from a separate introduction (Milnes et al. 2016; Hedstrom et al. 2017).

Given that *T. japonicus* is an oligophagous foreign species for which field release has not been permitted, its intentional movement across state lines is not allowed. Thus, biological control programs aiming to use this species can only be initiated once it is detected in the field in a given state. We set out to assess the presence of *T. japonicus* and current levels of parasitism and predation by native species by deploying sentinel egg masses of *H. halys* at a network of sites across southern Michigan. In addition, we deployed sentinel eggs of native stink bug species that were shown to be attacked in the laboratory by *T. japonicus* to assess non-target effects in field settings. We report the first record of *T. japonicus* in Michigan and find no evidence of non-target parasitism. The detection and capture of live individuals now allows for a biological control program to be mounted against *H. halys* in Michigan.

Materials and Methods

We deployed sentinel egg masses of *H. halys* between May and October 2018 (Fig. 1). Egg masses were collected from laboratory colonies maintained at Michigan State University (initial propagule provided by the New Jersey Department of Agriculture: Beneficial Insects Facility). To test for non-target parasitism in the field we also deployed egg masses of two species of native stink bugs, *Podisus maculiventris* (Say) and *Thyanta custator* (Fab.), which were shown to be successfully parasitized by *T. japonicus* in laboratory studies.

Egg masses were deployed in ten locations (Fig. 1) across central and western Michigan in the primary fruit and vegetable growing region of Michigan where *H. halys* populations have been most prevalent since its arrival in the state. The sites consisted of a diversity of cropping systems, including apples, blueberries, and farms with mixed crops. All sites had large non-agricultural areas nearby in the form of adjacent wood lots or fallow fields. A description of the sites and the number of sentinel egg masses of each species at each site is listed in Table 1. Native stink bug and *H. halys* egg masses were deployed following the protocol of previous sentinel egg mass programs in the eastern United States (Ogburn et al. 2016). Due to fluctuations in egg mass availability, the monitoring period of each site differed (Table 1). Either fresh egg masses laid within a 24-hour period or frozen (at –80˚ C for three minutes) eggs were deployed. Eggs were left in the field for 2–3 days and then brought back to the laboratory and kept at 20°C until nymphs or parasitoids had emerged. Any parasitoids that emerged from the sentinel egg masses were identified using the identification tools of Talamas et al. (2015a).

Eggs deployed early in the season (N = 142) at 3 sites (ENG, W, TR) from May through July were assessed for signs of natural enemy attack (both parasitism and predation). Eggs deployed during this earlier period were left in the field for 48 hrs, after which they were collected and assessed for signs of natural enemy attack using a compound microscope. This was conducted using the protocols of Ogburn et al. (2016) with the exception that egg masses were not dissected to check for partially developed parasitoids or other signs of unsuccessful parasitism. Six weeks after nymph emergence, egg masses were reassessed to determine hatch rate, and to check for emerged parasitoids. During this period, many egg masses became too moldy to assess from accumulated moisture whilst

Table 1: Sites where sentinel egg masses were deployed. Details of the main crop and the number of egg masses from each stink bug species are listed, as well as the first and last date on which egg masses were deployed. Egg mass numbers in parentheses are the number of frozen egg masses deployed.

Site	Crop	*H. halys*	*P. maculiventris*	*T.custator*	Start	End
SOF	Mixed	78 (10)	23 (2)	2 (0)	08/14/18	09/28/18
EF	Mixed	20 (9)	7 (1)	4 (2)	08/14/18	09/25/18
DG	Mixed	38 (0)	0	0	09/13/18	10/05/18
BT	Blueberry	1 (1)	3 (3)	1 (1)	09/14/18	09/14/18
ENG	Apple	25 (7)	0	0	05/23/18	08/15/18
W	Mixed	8 (0)	0	0	06/13/18	06/15/18
TR	Mixed	14 (7)	0	0	05/22/18	06/14/18
DG	Mixed	38 (0)	0	0	09/13/18	10/05/18
L	Blueberry	2 (2)	4 (4)	0	09/04/18	09/17/18
K	Blueberry	2 (1)	2 (2)	1 (1)	09/04/18	09/17/18
H	Blueberry	1 (1)	3 (3)	1 (1)	09/14/18	09/14/18

Table 2: All parasitoid emergences from sentinel egg masses. All sentinel egg masses that were parasitized by native parasitoids were frozen.

Site	Sentinel egg mass species	Date deployed	Date retrieved	Parasitoid species	Number of individuals
ENG	*H. halys*	05/23/18	05/25/18	*Trissolcus euschisti*	2 (2 males)
W	*H. halys*	06/13/18	06/15/18	*Trissolcus brochymenae*	5 (5 males)
ENG	*H. halys*	07/09/18	07/11/18	*Trissolcus euschisti*	9 (2 males)
SOF	*H. halys*	08/14/18	08/16/18	*Trissolcus japonicus*	5 (2 males)

deploying egg masses during rainy weather. Any egg masses that were too moldy to assess were discarded and are not included in the data presented here. Later in the season from August through October most sentinel egg placements focused around the area where *T. japonicus* had been captured and only rates of parasitism were assessed due to time constraints (Table 1).

Results

Trissolcus japonicus emerged from a single *H. halys* eggs mass that was deployed on 14 August 2018 at the Michigan State University Student Organic Farm (site code: SOF) three miles south of the East Lansing campus. A fresh egg mass was attached to a paw-paw tree (Magnoliales: Annonaceae, *Asimina triloba*, Dunal) located in an organic garden that included a diversity of native and imported tree species, many weeds, and ornamental and agricultural crop species including peaches, grapes, and raspberries. Three male and two female *T. japonicus* individuals emerged 23 days later on 6 September 2018.

Of the 142 egg masses deployed to measure natural enemy attack rate, eight were lost during deployment and 14 became too moldy to assess, leaving a total of 120 egg masses containing 3239 individual *H. halys* eggs. These egg masses contained an average of 27.0 eggs and of these an average of 9.06 eggs successfully emerged as nymphs (33.5% hatch rate). Chewing predation occurred on three egg masses, affecting ten eggs in total (2.5% of egg masses, 0.3% of individual eggs). Incomplete chewing predation (like that associated with spider feeding, Morrison et al. 2016) occurred on 12 egg masses, affecting 34 eggs (10.0% of egg masses, 1.05% of individual eggs). Sucking predation associated with hemipteran predators occurred on seven egg masses affecting 13 individual eggs (5.22% of egg masses, 0.4% of individual eggs). Parasitism occurred on three egg masses from two different species with a total of 12 adult parasitoids that successfully emerged from parasitized eggs (2.1% of egg masses, 0.4% of individual eggs). Including all 189 *H. halys* egg masses and both native and non-native parasitoids, the overall parasitism rate was 2.1%. Only native parasitoids emerged from these eggs, *Trissolcus brochymenae* (Ashmead) and *Trissolcus euschisti* (Ashmead). All emerging parasitoids from sentinel eggs are detailed in Table 2, with the site and dates the sentinel egg masses were deployed, and the number and species of emerging parasitoids.

Discussion

The discovery of *T. japonicus* in Michigan will have a major impact on the way *H. halys* is managed in the state. Currently, pesticides are the primary tactic used to combat the pest; however, now a classical biological control program can be initiated as in New York and Oregon where mass rearing and release of *T. japonicus* are already underway (BMBS SCRI Annual Report 2017). We captured *T. japonicus* at an organic farm, despite deployment of eggs at the edges of numerous conventionally managed orchards and mixed farms, which suggests that pesticide applications might negatively affect this parasitoid and limit its potential as a biological control agent in some cropping areas (Wilkinson et al. 1975, Croft 1990, Ndakidemi et al. 2016), although Kaser et al. (2018) recorded *T. japonicus* in a managed peach orchard. Further research is therefore required in order to determine how current chemical control regimes could be amended to form an integrated pest management strategy for *H. halys* that complements classical biological control by *T. japonicus* (Roubos et al. 2014).

Our discovery of *T. japonicus* indicates continued westward range expansion from the east coast. This is also one of the northernmost records of *T. japonicus* east of the Rocky Mountains. Despite its cold winter weather, Michigan falls into the predicted range suitable for *T. japonicus* (Avila and Charles 2018) and it is therefore likely that *T. japonicus* populations will continue to persist, at least in the southern half of the state.

Currently, *T. japonicus* has not been approved for release in the United States or permitted for interstate redistribution largely due to its potential to attack native stink bug species, such as *P. maculiventris*, which is a predatory stink bug and an important biological control agent in its own right (Botch and Delfosse 2018). In the laboratory, *T. japonicus* shows strong preference for *H. halys* eggs and often rejects non-target species for oviposition but only when it is reared on its primary host (Botch and Delfosse 2018). Attack on non-target species was shown to increase with prior exposure to native stink bugs but also resulted in decreased brood and adult sizes of *T. japonicus*. We deployed sentinel egg masses from native stink bugs throughout the state including the place where *T. japonicus* was detected but did not find any signs of non-target attacks. These results might suggest that *T. japonicus* prefers *H. halys* over native stink bugs in the field. However, the number of sentinel egg masses was relatively low and additional replication of both *H. halys* and native stink bug egg masses is required to better understand the distribution and population sizes of *T. japonicus* in Michigan and its realized host range in the field.

We found two native congeners, *T. brochymenae* and *T. euschisti* emerging from frozen egg masses and overall very low natural enemy utilization of *H. halys* eggs by native species. This is congruent with previous studies reporting parasitism rates of less than 5% and predation rates between 4.4–12.7% (Ogburn et al. 2016, Cornelius et al. 2016, Abram et al. 2017). Frozen eggs are thought to be more susceptible to parasitism from native parasitoids (Herlihy et al. 2016) because the eggs cannot mount an immune response and defend themselves once the hosts have ceased development (Haye et al. 2015). Despite our small sample size, we found that native parasitoids only emerged from frozen *H. halys* egg masses. The two species we caught, *T. euschisti* and *T. brochymenae*, are both common parasitoids of sentinel *H. halys* egg masses across the United States, but frequently fail to complete development on live *H. halys* eggs (Abram et al. 2017). We did not dissect egg masses to assess for parasitism but only measured parasitoid emergence, which likely underestimated the rate of parasitism and the non-reproductive effects native parasitoids have on *H. halys* populations (Abram et al. 2018). The fact that native parasitoids attack *H. halys* egg masses, and that a small proportion do emerge as adult parasitoids, suggests native parasitoids have the potential to exploit *H. halys* as hosts but require additional adaptations. Thus, *H. halys* populations could grow largely unchecked in North America and *T. japonicus* may represent the only effective natural enemy to be used for biological control of this pest. Further work should focus on exploring the continued range expansion of *T. japonicus* and measuring its impact on *H. halys* populations both in managed and natural areas.

Acknowledgments

This work was supported by the USDA National Institute of Food and Agriculture, Hatch Project Nos. 1017601 and MICL02580 and Michigan State University AgBioResearch. It was also supported in part by the Florida Department of Agriculture and Consumer Services – Division of Plant Industry, and the USDA Farm Bill, Monitoring for the presence and impact of *Trissolcus japonicus*. We thank P. Fanning and C. Millan-Hernandez for logistics.

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First Records of the Adventive *Pseudoanthidium nanum* (Mocsáry) (Hymenoptera: Megachilidae) in Illinois and Minnesota, with Notes on its Identification and Taxonomy

Zachary M. Portman[1*], Skyler J. Burrows[2], Terry Griswold[3], Mike Arduser[4], Aaron J. Irber[1], Rebecca K. Tonietto[5], Daniel P. Cariveau[1]

[1] Department of Entomology, University of Minnesota, St. Paul, Minnesota

[2] Department of Biology, Utah State University, Logan, Utah

[3] USDA-ARS Pollinating Insects Research Unit, Logan, Utah

[4] Conservation Research Institute, Chicago, Illinois

[5] Department of Biology, University of Michigan-Flint, Flint, Michigan

*Corresponding author: (email: zportman@umn.edu)

Abstract

We report the first records of *Pseudoanthidium nanum* (Mocsáry) (Hymenoptera: Megachilidae) in Illinois and Minnesota in 2016 and 2018, respectively. This represents a relatively rapid expansion since *P. nanum* was first detected in New Jersey in 2008. In order to help monitor the spread of this bee, we provide information on how to identify *P. nanum* and provide images of the general habitus, diagnostic features, and male genitalia. Finally, we confirm the taxonomic identity of *P. nanum* in the United States and highlight potential impacts on native anthidiines.

Keywords: *Anthidium*, Anthophila, invasive species, Midwest, range expansion

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The number of non-native bees in North America continues to increase as new species are introduced and existing species expand from the point of introduction (Cane 2003, Sheffield et al. 2011, Russo 2016). Cavity-nesting bees, particularly those in the family Megachilidae, make up an outsized proportion of adventive bees due to the ease of inadvertent transport of their nests (Cane 2003, Russo 2016). Megachilids that have recently been introduced or expanded their ranges in North America include *Anthidium florentinum* (Fabricius) (Normandin et al. 2017), *A. manicatum* (L.) (Gibbs and Sheffield 2009), *A. oblongatum* (Illiger) (Miller et al. 2002), *Megachile sculpturalis* Smith (Hinojosa-Díaz et al. 2005), and *Osmia taurus* Smith (Giles and Ascher 2006). For many of these species, information about their spread and current distribution is sparse or lacking, hampering our understanding of their rate of spread and potential effects on native bees and ecosystems.

A species of *Pseudoanthidium* Friese, identified as *P. nanum* (Mocsáry, 1881), was first detected in the United States in New Jersey in 2008 (Droege and Shapiro 2011, Ascher et al. 2014). The native range of *P. nanum* encompasses Europe, western Asia, and the Middle East (Fateryga and Popov 2017, Kuhlmann et al. 2018). After its initial detection in New Jersey, *P. nanum* was subsequently detected in New York in 2009 (Matteson et al. 2013, Ascher et al. 2014) and Maryland in 2010 (Droege and Shapiro 2011). Finally, *P. nanum* was reported from Cleveland, Ohio in 2016 (Spring 2017). The distribution of *P. nanum* in the United States appears to be restricted to urban and industrial areas (Droege and Shapiro 2011).

The genus *Pseudoanthidium* contains approximately 60 described species (and numerous undescribed species) divided among 12 subgenera (Litman et al. 2016). They are native to Europe, Asia, and Africa, with no native species in the New World or Australia (Michener 2007). The genus contains at least one additional species that has spread outside its native range (Russo 2016). *Pseudoanthidium repetitum* (Schulz), native to South Africa, was first detected in Australia in 2000, and has since spread rapidly and become one of the most common bees in some areas (Baumann et al. 2016). The invasion and rapid spread of *P. repetitum* has been attributed to its affinity for nesting in a wide range of man-made structures, especially meter-boxes and window frames (Baumann et al. 2016, Queensland Museum 2018).

Here, we present the first records of *P. nanum* in Illinois and Minnesota and confirm its taxonomic identity. These new speci-

Table 1: *Pseudoanthidium nanum* specimens examined from the United States.

Institution	Specimen ID	State	Year	Original Study
AMNH	AMNH_BEE00131649	New York	2009	Matteson et al. 2013
BBSL	DRO167202	Maryland	2010	Droege and Shapiro 2011
BBSL	DRO167193	Maryland	2010	Droege and Shapiro 2011
AMNH	AMNH_BEE00231799	New Jersey	2011	Ascher et al. 2014
AMNH	AMNH_BEE00231798	New Jersey	2011	Ascher et al. 2014
AMNH	AMNH_BEE00076577	New Jersey	2011	Ascher et al. 2014
AMNH	AMNH_BEE00290799	New Jersey	2011	Ascher et al. 2014
AMNH	AMNH_BEE00290786	New Jersey	2011	Ascher et al. 2014
Tonietto Lab/ INHS	20162340	Illinois	2016	This study
Tonietto Lab/ INHS	201610027	Illinois	2016	This study
Cariveau Lab/ UMSP	urb18-0723	Minnesota	2018	This study

mens match other specimens of *P. nanum* from the eastern United States, indicating a rapid spread across the country. We provide detailed images of the key identifying features of *P. nanum* in order to facilitate the identification and monitoring of this adventive species. Lastly, we highlight the fact that *P. nanum* is a member of a poorly understood species complex synonymized under the unavailable name *P. lituratum* (Panzer) by Warncke (1980) and frequently referenced by that name (Přidal 2004, Kuhlmann et al. 2018) and we confirm that the specimens in the United States match *P. nanum* as it was originally described in Europe (Mocsáry 1881).

Methods and Materials

Specimens examined for this study included novel collections from the midwestern United States, previously reported specimens from the eastern United States (Table 1), and specimens from the native range of *P. nanum* in Europe. The Minnesota specimen was collected in 2018 as part of a broader survey of the pollinators of urban gardens. Resources used to initially identify the bees included the USDA Exotic Bee ID Key (Burrows et al. 2018) and images from Droege and Shapiro (2011). The Minnesota specimen currently resides in the Cariveau Lab insect collection (University of Minnesota) and will be permanently deposited in the University of Minnesota Insect Collection (UMSP) in St. Paul, Minnesota. The two Illinois specimens were collected in 2016 as part of a broader study on urban garden pollinators. They are currently in the Tonietto lab collection (University of Michigan, Flint) and will be permanently deposited at the Illinois Natural History Survey (INHS) in Urbana, Illinois. Additional material was examined from the American Museum of Natural History (AMNH) in New York City, New York and the Pollinating Insects Research Unit (BBSL) in Logan, Utah.

Classification of *Pseudoanthidium* follows Litman et al. (2016). For the nomenclature of *P. nanum* (Mocsáry, 1881) we use a description year of 1881. The years 1879 and 1881 have both been used to refer to *P. nanum*, sometimes even in the same publication (e.g. Přidal 2004). We use the date of 1881 because that is when the volume of the journal was completed (see Baker 1996). The abbreviations S1…S8 and T1…T7 are used for sterna and terga, respectively. Photographs were taken using two systems: an Olympus DP27 camera mounted on an Olympus SZX16 stereomicroscope and a Keyence VHX-5000 microscope imaging system with a VH-Z20R lens and a VHX-S550E stand. Images from the Olympus camera were stacked using CombineZP software (Hadley 2010) and all photographic plates were compiled using Adobe Photoshop 2018 software (Adobe Systems Inc., San Jose, CA).

Results and Discussion

Details of the specimens from Illinois and Minnesota. Two *P. nanum* specimens, one male and one female, were collected in Illinois in 2016. The male, specimen number 20162340, was collected on 29 June 2016 in a pan trap by Elizabeth Kosson, Kristian Williams, and Nick Olson at Windy City Harvest Legends Farm, Chicago, Cook County, Illinois (41.812, –87.628). The female, specimen number 201610027, was collected in a pan trap on 26 Aug 2016 by Elizabeth Kosson, Kristian Williams, and Nick Olson at Windy City Harvest Rodeo Farm, Chicago, Cook County, Illinois (41.844, –97.691).

A single male *P. nanum* (Fig. 1), specimen number urb18-0723, was collected with a hand net from *Erigeron* sp. on 13 June 2018 by Aaron Irber at Corcoran Communi-

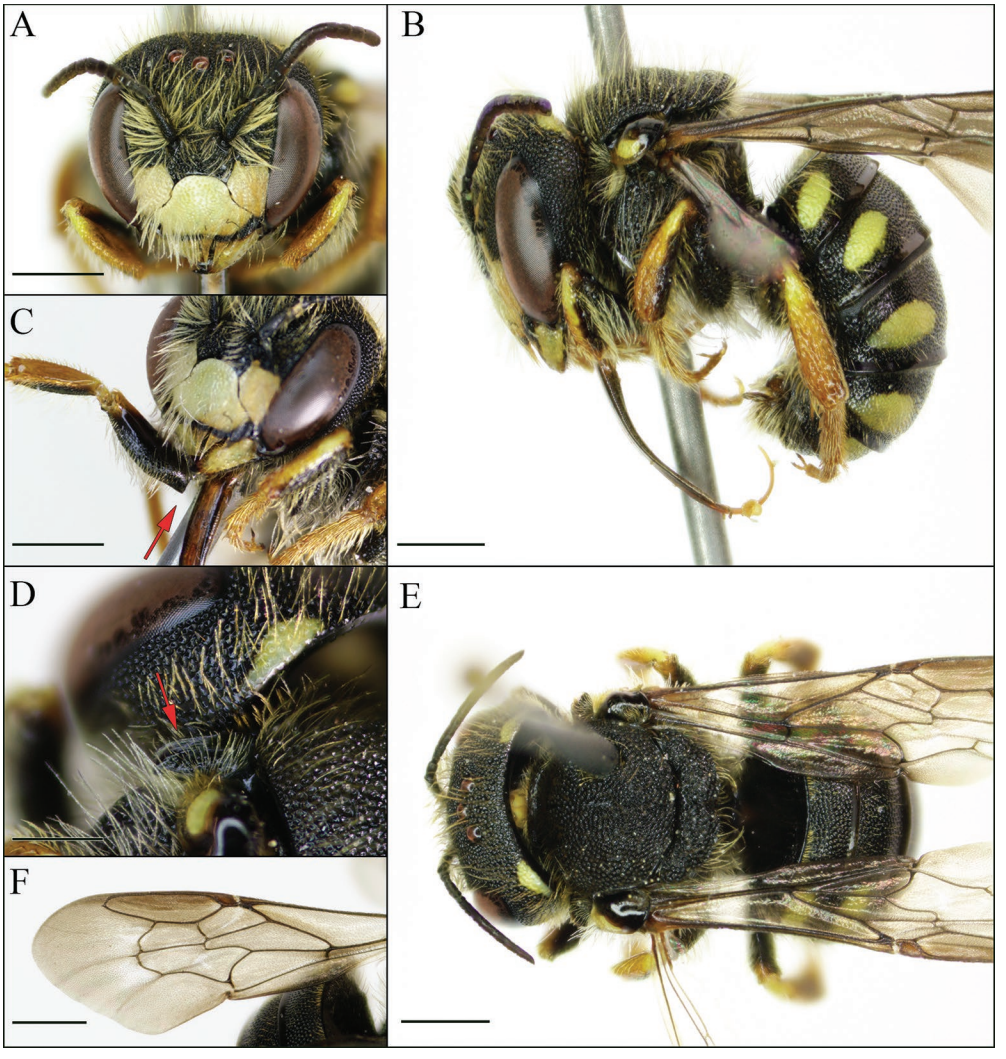

Figure 1: *Pseudoanthidium nanum* male: A) face B) body, lateral view C) conical-shaped base of fore-femur D) lamellate pronotal lobe E) body, dorsal view F) forewing. All scale bars = 1 mm, except 500 µm in D.

ty Garden, Minneapolis, Hennepin County, Minnesota (44.9428, −93.2368).

Identification of *Pseudoanthidium nanum* in the United States. Male *P. nanum* can be distinguished from other US anthidiini by a combination of the following diagnostic characters: lamellate ridge on the pronotal lobes (Fig. 1D), lateral combs on S5, and an apico-medial brush of long, wavy hairs on S3 (Fig. 2). Female *P. nanum* (Fig. 3) are more difficult to recognize, but they can be diagnosed by the following combination of characters: lamellate ridge on the pronotal lobes (as in Fig. 1D), fore-femur with conical base (Fig. 3C), 5 mandibular teeth, and the lack of arolia. These characters are all shared by males, except males have 3 mandibular teeth.

In addition to the diagnostic characters listed above, the following characters can help differentiate *Pseudoanthidium* from similar-looking species in the US: presence of scopal hairs on sterna in the female (Fig. 3B), presence of yellow maculations on the body (Figs. 1B, 3B), forewing with darkened marginal cell (Fig. 1F), anterior face of T1 smooth and divided from the posterior face by a small carina (Fig 1E), and a rounded

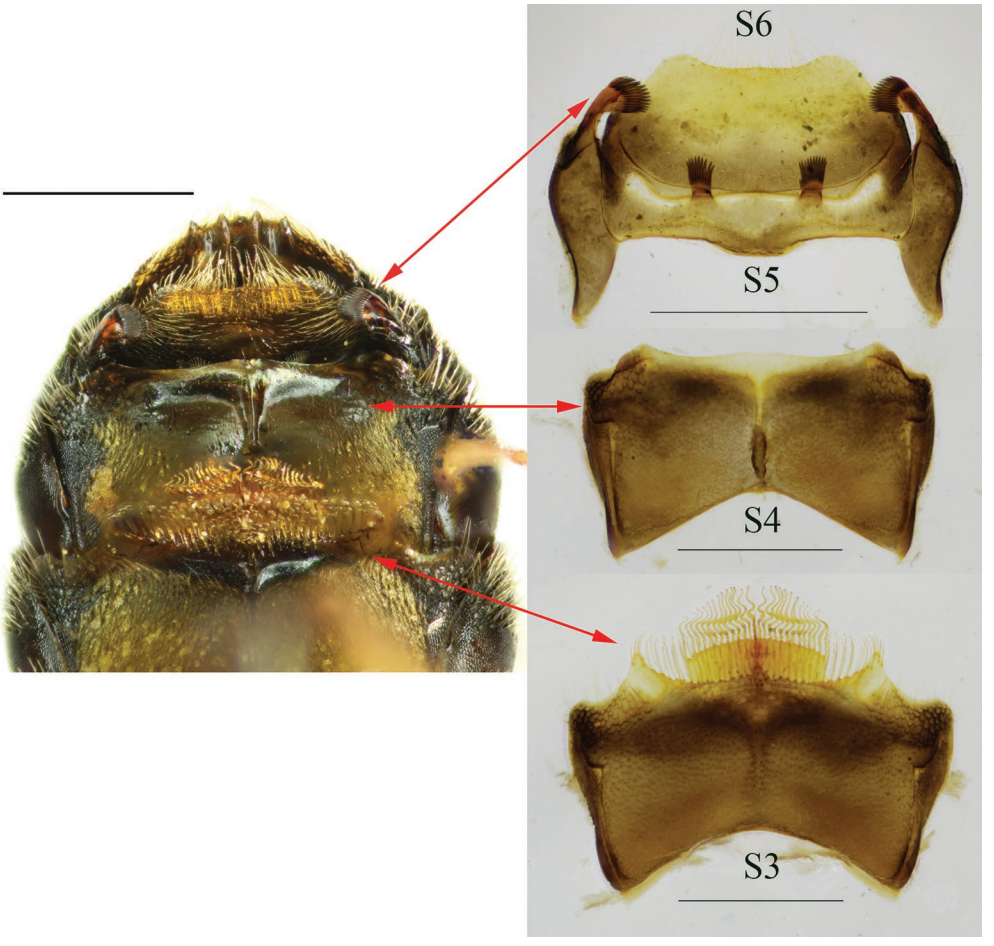

Figure 2: *Pseudoanthidium nanum* male apical sternites (S3–6) showing the diagnostic S3 hair brush and S5 lateral combs. All scale bars = 1 mm.

omaulus (surface between the lateral and anterior faces of the mesepisternum). In addition, the females have a distinct pattern of punctures on the clypeus, starting with relatively large punctures basally, with the punctures becoming gradually more minute and contiguous towards the apical margin (Fig. 3A).

In the United States, *P. nanum* is most likely to be confused with the genus *Anthidium* because the two genera look similar and share multiple characters. Indeed, *Pseudoanthidium* keys out to *Anthidium* in Mitchell (1962) due to the lack of pygidial plate, extensive yellow maculations, and lack of arolia. *Pseudoanthidium nanum* can be separated from all native *Anthidium* by the presence of a raised lamellate ridge on the pronotal lobes (Fig. 1D), however, it can be confused with a non-native *Anthidium* species, *A. oblongatum*, which also has a lamellate pronotal lobe (Miller et al. 2002, Gonzalez and Griswold 2013). Female *P. nanum* can be definitively separated from *A. oblongatum* by the number of mandibular teeth: *P. nanum* only has 5 teeth, whereas *A. oblongatum females* have 9–12 teeth. Male *P. nanum* can be separated from *A. oblongatum* (and all other North American Megachilidae) by the pair of lateral combs on S5 and hair brush on S3 (Fig. 2). In addition, male *P. nanum* have a conical projection on the fore-femur (Fig. 1C) and lack spines or protrusions on their apical terga, except for a minute medial nub on T7 (Fig. 4C). In contrast, *A. oblongatum* lacks a conical projection on the fore-femur and has lateral and medial spines on T6 and a broad medial emargination on T7 (illustrated in Fig. 254 of Gonzalez and Griswold 2013). Finally, *P. nanum* can be distinguished from all *Anthidium* in eastern North America, both native

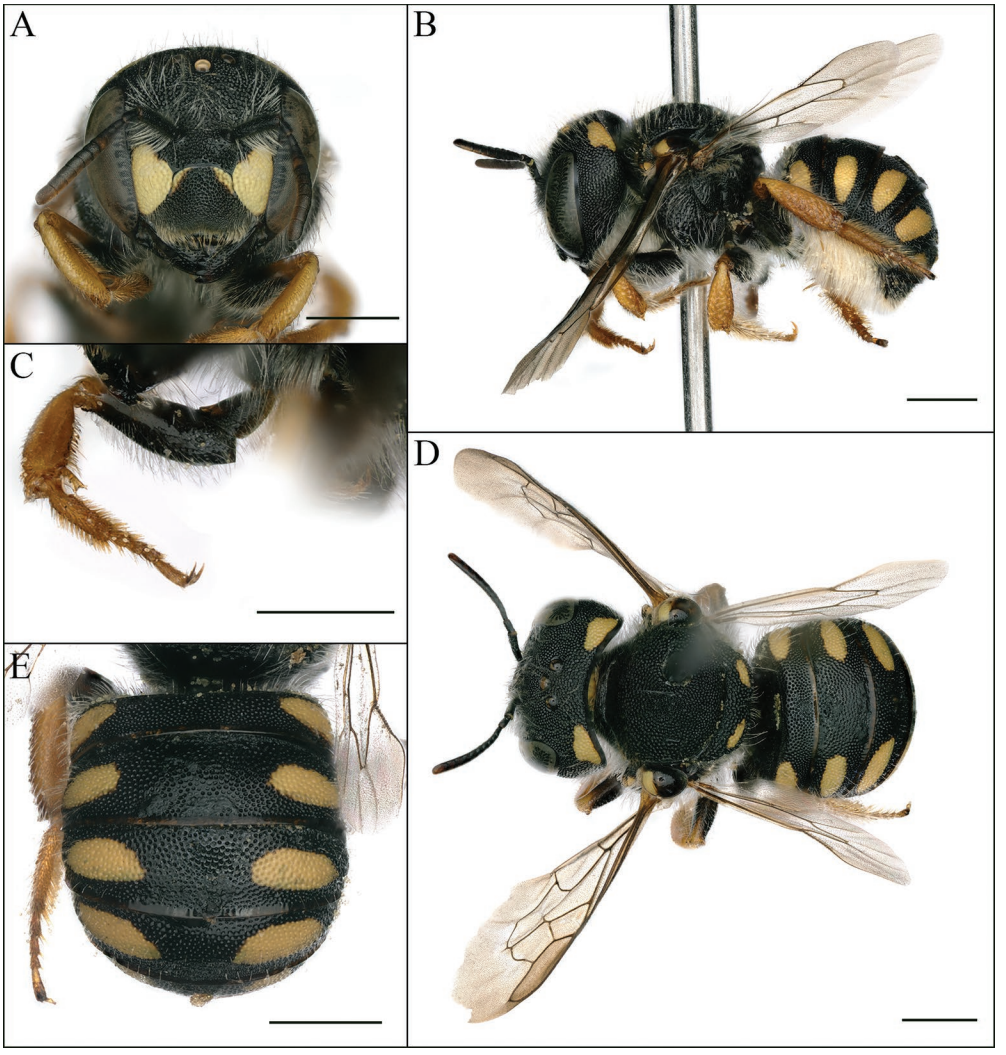

Figure 3: *Pseudoanthidium nanum* female: A) face B) body, lateral view C) conical-shaped base of fore-femur D) body, dorsal view E) abdomen, dorsal view. All scale bars = 1 mm.

and exotic, by the small body size (5–7 mm body length).

The distinctive structure of the genitalia and hidden sterna of male *P. nanum* alone distinguishes it from all North American bees (Fig. 4). Features of the genitalia not readily apparent from the figure include: 1) the inner margins of the penis valves have fine hairs that extend along the entire inner length, except subapically where there are two stronger hairs on the left valve and one on the right valve; 2) the gonostyli have a dorsal carina that extends along their lateral margin for nearly all their length; and 3) the area between the penis valves appears more rectangular in the dorsal view (Fig. 4A) because the endophallus is slightly everted; the more horseshoe-shaped area between the penis valves as seen in the ventral view is closer to the "true" form (Fig. 4B).

The taxonomic identity of *Pseudoanthidium nanum* in the United States. Although the taxonomy of *Pseudoanthidium* contains unresolved issues, we confirm the specimens in the US can be assigned to *P. nanum*. In short, *P. nanum* is a member of species complex, generally referred to as the "*lituratum* group," that contains multiple

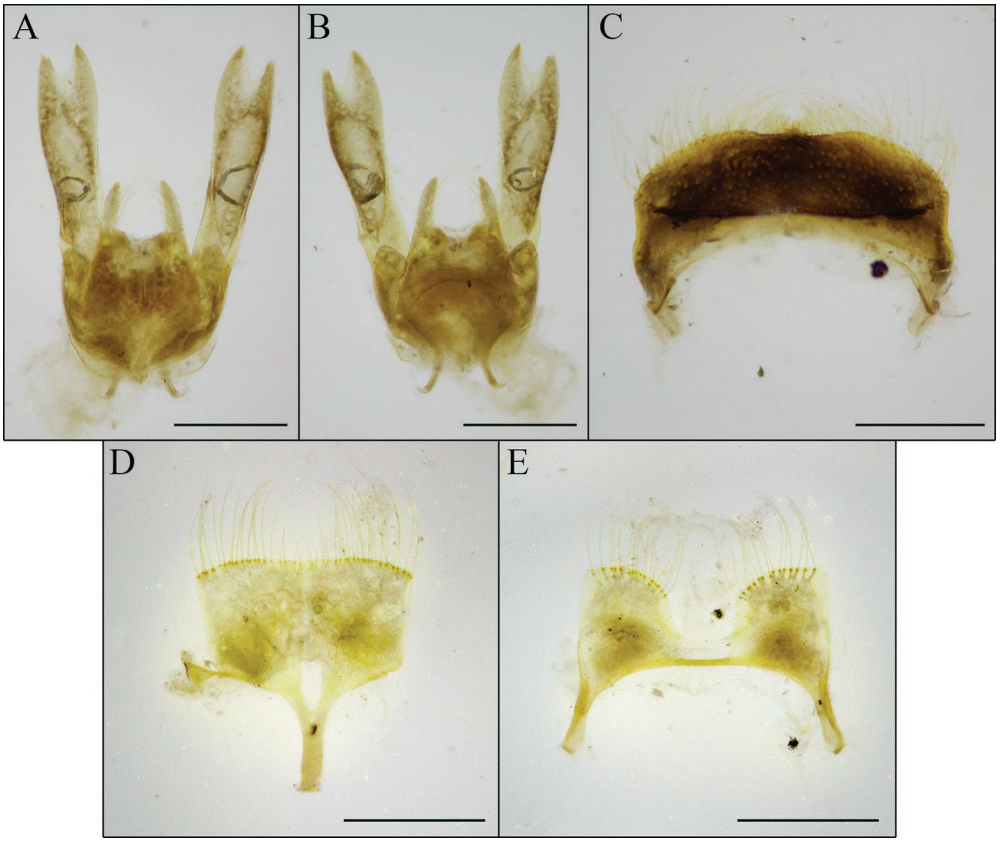

Figure 4: *Pseudoanthidium nanum* male A) genitalia, dorsal view, B) genitalia, ventral view, C) T7 D) S8 (right point of attachment broken off) E) S7. All scale bars = 500 μm.

closely-related species of unsettled taxonomic status (Přidal 2004, Kuhlmann et al. 2018). Adding to the confusion, although *P. lituratum* (Panzer) is not a valid name because it is a primary homonym (Přidal 2004, Aguib et al. 2010, Kuhlmann et al. 2018), it is still often used in the literature (e.g. Přidal 2004, Bogusch et al. 2017, Gonzalez et al. 2017). However, based on examination of specimens from the type locality of *P. nanum* originally determined by Mocsáry, we believe that the specimens in the United States correspond with *P. nanum* as originally defined (Mocsáry 1881). Specifically, Terry Griswold has examined a series of *P. nanum* in the Hungarian National History Museum originally determined by Mocsáry. Two permanently borrowed specimens from that series deposited in the BBSL collection were compared to US specimens; the locality for these two Mocsáry specimens is "Hungariae meridionalis comitatu Temesiensis," which matches the original type locality of *P. nanum*, though they are not old enough to be a part of the original type series.

Although the *P. nanum* in the US agree morphologically with the original definition of *P. nanum*, the specimens of *P. nanum* in our possession would not appear to match *P. nanum* as defined by Aguib et al. (2010). Specifically, in the US specimens, the structure of the lateral combs on S5 differs from that shown by Aguib et al. (2010) and the penis valves are more widely separated and less tapering. Study of Aguib et al.'s (2010) image of the S5 comb suggests it was taken at an oblique angle which could account for the disparity in shape. More clarity must await a broader taxonomic revision of the *lituratum* species group. Towards this end we provide images of the genitalia and apical sterna (Figs. 2 and 4), to illustrate our concept of Mocsáry's species and to assist in future taxonomic evaluation of the *lituratum* species group.

Other invasive Anthidiini in the North Central United States. In addition to *P. nanum*, there are already two other non-native anthidiine bees established in the North Central US: *A. manicatum* and *A. oblongatum*. *Anthidium manicatum* was first detected in the US in New York State in 1963 (Jaycox 1967), though it was not found in the Midwest until it was detected in Ohio in 1997 (Miller et al. 2002). Its range has increased rapidly since then, with new records in Illinois, Wisconsin, Idaho, California, and Colorado in 2006 and 2007 (Tonietto and Ascher 2008, Gibbs and Sheffield 2009). The timing of the arrival of *A. manicatum* in MN is not clear, with the first recorded specimens in the UMSP collection from 2013, though postings on BugGuide.net place it as early as 2008 (https://bugguide.net/node/view/199661).

Anthidium oblongatum is also a recent arrival to the North Central US. It was first found in northeastern US in 1994 (Hoebeke and Wheeler 1999). It was collected in Ohio in 2000, in Illinois in 2008, and in Michigan in 2010 (Miller et al. 2002, Tonietto and Ascher 2008, O'Brien et al. 2012). In Minnesota, the earliest collected specimens of *A. oblongatum* in the UMSP collection are from 2015, though there is a 2013 record of the bee from BugGuide.net (https://bugguide.net/node/view/804727).

Implications for native bees. It is unclear what effect *P. nanum* and other invasive anthidiines may have on the native bee fauna of the North Central US. Of particular concern are native anthidiines that are already rare in the North Central US, such as *A. psoraleae* Robertson and *A. tenuiflorae* Cockerell. Both species are largely western in distribution and are rare in the North Central US (Grundel et al. 2011, O'Brien et al. 2012, Gonzalez and Griswold 2013, Gibbs et al. 2017). However, given that *P. nanum* and the two invasive *Anthidium* species appear to be largely restricted to disturbed areas, their effects should be limited (Gibbs and Sheffield 2009, Droege and Shapiro 2011, Miller et al. 2002). In addition, *P. nanum* is likely a specialist on the pollen of Cynareae (Müller 1996, Gonzalez et al. 2017), further reducing its potential impact. However, given that *P. nanum* nests in stems and a variety of other cavities such as galls and snail shells (Litman 2012), it could potentially compete with native bees for nest sites. Finally, *P. nanum* and other non-native bees could be involved in spreading pests and disease to native bees, a largely hidden factor which is gaining increasing recognition as a major threat to native bee health (Colla et al. 2006, Murray et al. 2018).

Conclusion

It is important to monitor *P. nanum* in North America to better understand and predict its potential spread and impacts on native bees. Its presence in Minnesota represents a rapid range expansion from the initial area of introduction since it was first detected in New Jersey in 2008 (Droege and Shapiro 2011). This relatively rapid rate suggests that the bee will continue to spread across North America, a hypothesis supported by two unconfirmed reports of *P. nanum* in Oregon in 2018 on BugGuide and iNaturalist (https://www.inaturalist.org/observations/14356133, https://bugguide.net/node/view/1566202). However, we are reluctant to classify these unconfirmed reports as *P. nanum* due to the difficulty of identifying this species from photographs and because the West Coast distribution could possibly represent a separate introduction event. It is our hope that the resources provided here will assist in the identification and monitoring of *P. nanum* since it appears likely to continue to expand its range.

Finally, the unsettled taxonomy of *Pseudoanthidium* and previous uncertainty surrounding the species identity of *P. nanum* in the United States highlights the importance of basic taxonomy and the need for identification tools to monitor invasive species. As this species demonstrates, even in areas of the world with well-known bee faunas and hundreds of years of taxonomic history, there remains a substantial amount of work to be done (Gonzalez et al. 2013). In this case, it is important to confirm the species identity in order to compile accurate information on the biology and native range of *P. nanum*.

Acknowledgments

We thank Chelsey Ritner for taking photographs of female specimens, Kristian Williams, Elizabeth Kosson and Nick Olsen for fieldwork assistance, and Paige Muñiz for identification assistance. We are grateful to Corcoran Community Garden in Minneapolis, MN for allowing sampling as well as Windy City Harvest in Chicago, IL for permission to conduct research at Rodeo and Legends farms. We are grateful to the two anonymous peer reviewers for their constructive comments. Funding to SJB was provided by USDA-APHIS under cooperative agreements 16-8130-0736-CA and AP17PPQS&T00C053, all work in Chicago was funded by a David H. Smith postdoctoral research fellowship awarded to RKT, and work in Minnesota was funded by grant to DPC through the Minnesota Environment

and Natural Resources Trust Fund M.L. 2016, Chp. 186, Sec. 2, Subd. 03a.

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Historical Population Increases and Related Inciting Factors of *Agrilus anxius, Agrilus bilineatus,* and *Agrilus granulatus liragus* (Coleoptera: Buprestidae) in the Lake States (Michigan, Minnesota, and Wisconsin)

Robert A. Haack and Toby R. Petrice
USDA Forest Service, Northern Research Station, 3101 Technology Blvd., Suite F, Lansing, MI 48910
e-mail: robert.haack@usda.gov (emeritus) and toby.petrice@usda.gov

Abstract

Three native species of tree-infesting *Agrilus* (Coleoptera: Buprestidae) have regularly reached outbreak levels in the Lake States (Michigan, Minnesota, and Wisconsin), including *A. anxius* Gory (bronze birch borer), *A. bilineatus* (Weber) (twolined chestnut borer), and *A. granulatus liragus* Barter & Brown (bronze poplar borer). The main host trees for these *Agrilus* are species of *Betula* for *A. anxius*, *Castanea* and *Quercus* for *A. bilineatus*, and *Populus* for *A. granulatus liragus*. Based on 197 annual forest health reports for Michigan (1950–2017, 66 years), Minnesota (1950–2017, 64 years), and Wisconsin (1951–2017, 67 years), *A. bilineatus* was the most often reported *Agrilus* species in all three states (mentioned in 90 annual reports), with *A. anxius* second (71 reports) and *A. granulatus liragus* third (21 reports). Drought was the most commonly reported inciting factor for outbreaks of all three *Agrilus* species, with defoliation events ranking second. The top two defoliators reported as inciting outbreaks of each species were, in decreasing order, *Fenusa pumila* Leach (Hymenoptera: Tenthredinidae; birch leafminer) tied with *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae; forest tent caterpillar) for *A. anxius*; *M. disstria* and *Alsophila pometaria* (Harris) (Lepidoptera: Geometridae; fall cankerworm) for *A. bilineatus*; and *M. disstria* and *Choristoneura conflictana* (Walker) (Lepidoptera: Tortricidae; large aspen tortrix) for *A. granulatus liragus*. Other environmental factors occasionally listed as inciting *Agrilus* outbreaks included late spring frosts, ice storms, and strong wind events.

Keywords: Jewel beetles, flatheaded borers, aspen, birch, oak, environmental stress, outbreak

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The genus *Agrilus* (Coleoptera: Buprestidae) is considered the most speciose in the Animal Kingdom with over 3200 recognized species worldwide as of April 2019 (Jendek and Poláková 2014; E. Jendek, pers. comm.). The continental United States is known to have at least 194 recognized *Agrilus* species and subspecies, of which 13 species are exotic to the USA (Chamorro et al. 2015; Hoebeke et al. 2017, DiGirolomo et al. 2019). In the Lake States [a collective term for Michigan (MI), Minnesota (MN), and Wisconsin (WI)] there are at least 60 known *Agrilus* species, of which 4 are exotic (Wellso et al. 1976, Jendek 2013a, 2014).

Among the native tree-infesting *Agrilus*, there are three species that regularly reach outbreak levels in the Lake States: *Agrilus anxius* Gory (bronze birch borer), *A. bilineatus* (Weber) (twolined chestnut borer), and *A. granulatus liragus* Barter & Brown (bronze poplar borer) (Millers et al. 1989). They are similar in size (adults are about 7–11 mm long) and have similar life histories with the most significant difference being their larval host plants: *A. anxius* on *Betula* (birch), *A. bilineatus* on *Castanea* (chestnut) and *Quercus* (oak), and *A. granulatus liragus* on *Populus* (aspen, cottonwood and poplar) (Solomon 1995). Each species is known to infest overmature trees as well as trees stressed by drought, defoliation, and other factors (Dunbar and Stephens 1976, Dunn et al. 1986, Millers et al. 1989, Haack and Acciavatti 1992, Solomon 1995, Muilenburg and Herms 2012, Haack and Petrice 2020).

Several life-history studies have been conducted on *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* in eastern North America (Balch and Prebble 1940, Barter and Brown 1949, Barter 1957, 1965, Carlson and Knight 1969, Cote and Allen 1980, Haack and Benjamin 1982, Loerch and Cameron 1984, Muilenburg and Herms 2012). Their life cycle is generally completed in one year, but at times two years are needed, especially when summers are cool or when eggs are laid on vigorous host trees or laid during

late summer. In the Lake States, or other areas of similar latitude, adult emergence of these three species usually starts in late May or early June, peaks in late June, and then diminishes through July and August. Adults feed on host foliage for several days to become sexually mature and then mate and oviposit in bark cracks and crevices along the major branches and trunks of host trees. Eggs are laid singly or in small clusters. Upon eclosion, larvae tunnel through the bark and feed in the cambial region, constructing zig-zag galleries that score both the inner bark (phloem) and outermost sapwood (xylem). There are four larval instars and larvae often enter the outer sapwood to molt. In late summer and autumn, mature last-instar larvae construct individual pupal cells in the outer sapwood on thin-barked trees, which is common in *Betula* and *Populus*, or in the outer bark on trees with thick bark, which is common in *Castanea* and *Quercus*. Pupation occurs in late spring and early summer. Newly formed adults exit through the bark by creating D-shaped exit holes that are characteristic for the genus. The sex ratio of emerging adults is about 1:1.

Over the past several decades many changes have occurred in the taxonomic status of these three *Agrilus* species. *Agrilus anxius* was initially described by Gory (1841), and included what we now refer to as *A. granulatus liragus*. Over a century later, Barter and Brown (1949) named *Agrilus liragus* as a new species, separating it from *A. anxius* based on color, male genitalia, and larval host plants. Carlson and Knight (1969) reevaluated the *Agrilus anxius* complex and reclassified *A. liragus* as a subspecies of *A. granulatus*. Later, Bright (1987) recognized *A. liragus* as a distinct species, then Nelson et al. (2008) once again recognized the subspecies *A. granulatus liragus*. Although both combinations have appeared in recent scientific literature, we use *A. granulatus liragus* in the present paper. *Agrilus bilineatus* was first described in 1801 under the name *Buprestis bilineata* Weber (Fisher 1928). For many years, two subspecies of *A. bilineatus* were recognized based on their larval hosts and subtle morphological differences, with *A. bilineatus bilineatus* larvae feeding in *Castanea* and *Quercus*, and larvae of *A. bilineatus carpini* Knull, feeding in *Carpinus* (hornbeam), *Fagus* (beech), and *Ostrya* (hophornbeam) (Knull 1923). This latter subspecies was later elevated to species status under the name *Agrilus carpini* Knull (Nelson and Hespenheide 1998). Given the above history, it is understandable that there has been some confusion in the literature on the actual larval hosts of these three *Agrilus* species.

Since the discovery of the Asian species *Agrilus planipennis* Fairmaire (emerald ash borer) in North America in 2002 and in European Russia in 2005 (Haack et al. 2002, 2015), there has been growing concern in Europe, as well as in other countries, that various exotic species of *Agrilus* could enter and greatly impact European urban and forest trees (Flø et al. 2015). For example, as of April 2019, EPPO (European and Mediterranean Plant Protection Organization) has conducted formal pest risk analyses (PRAs) for four *Agrilus* species, including *A. anxius* in 2010 (EPPO 2011), *A. planipennis* in 2013 (EPPO 2013), *A. bilineatus* in 2018 (EPPO 2019a), and *Agrilus fleischeri* Obenberger in 2018 (EPPO 2019b). We were team members of the Expert Working Groups that conducted the above four *Agrilus* PRAs: RAH for *A. anxius* and *A. planipennis* and TRP for *A. bilineatus* and *A. fleischeri*. During the PRAs for *A. anxius* and *A. bilineatus*, we provided the team members of the Expert Working Groups with details on the outbreak history of these two species in the Lake States, and in turn the team members encouraged us to summarize these data into a formal publication. In addition, the recent discovery of *A. bilineatus* in Turkey (Hızal and Arslangündoğdu 2018), has further increased interest in *A. bilineatus* and its potential threat to European *Castanea* and *Quercus* trees (EPPO 2019a, Haack and Petrice 2020). Given the above, we reviewed several decades of annual forest pest reports from the Lake States and recorded the number of times each native *Agrilus* species was mentioned as reaching pest status, as well as any biotic and abiotic factors that could have incited the outbreaks.

Materials and Methods

We reviewed all annual forest pest reports that we could locate from Michigan (1950–2017, 66 reports, missing 1951 and 1973), Minnesota (1950–2017, 64 reports, missing 1956, 1963, 1967, and 1973), and Wisconsin (1951–2017, 67 reports). Formal forest pest surveys, often involving aerial surveys, ground surveys, and on-site visits in response to calls from foresters and the public, have been conducted in Wisconsin since 1949, and in Michigan and Minnesota since 1950 (WI CD 1953). Therefore, our dataset represents nearly all published forest pest reports for these three US states. Moreover, in 1951, forest health staff from the Lake States met in Madison, WI, to coordinate their reporting and survey methods for forest pests of mutual concern (WI CD 1953), therefore we feel comfortable comparing infestation records across the Lake States. We located most reports in our USDA Forest

Table 1. Number of reports (and percent of the total reports) by state where *Agrilus anxius*, *A. bilineatus* or *A. granulatus liragus* were mentioned as being pests in the annual forest health reports published by the Departments of Natural Resources in Michigan (MI; 1950–2017), Minnesota (MN; 1950–2017), and Wisconsin (WI; 1951–2017).

	State		
Insect	**MI (66 reports)**	**MN (64 reports)**	**WI (67 reports)**
Agrilus anxius	11 (17 %)	33 (52 %)	27 (40 %)
Agrilus bilineatus	16 (24 %)	34 (53 %)	40 (60 %)
Agrilus granulatus liragus	7 (11 %)	11 (17 %)	3 (4 %)

Service library on the Michigan State University campus, where our Insect Research Unit has been located since 1956 (Haack 2006). For any missing years, we contacted the individual states, and in most cases they had copies available. Many of the reports since the 1990s are now online for the Lake States as well as all other US states (FHP 2018). Although the structure of state government has changed over time in the Lake States, these reports were typically prepared by the Forest Health staff within each state's Department of Natural Resources (DNR). The titles of these DNR reports changed over the decades, usually starting as *Forest Pest Reports* in the 1950s and 1960s, changing to *Forest Insect and Disease Report*s in the 1970s and 1980s, and then to *Forest Health Reports* in the 1990s to the present.

When reviewing each report, we looked for any mention of *Agrilus* beetles, either by scientific name or common name. We concentrated on native *Agrilus* species, but after discovery of the exotic species *A. planipennis* in each state (2002 in MI, 2008 in WI, 2009 in MN), *A. planipennis* was mentioned in every subsequent annual report. For each mention of a native *Agrilus* species, we recorded the year of the report, where in the state the species reached pest status, and information on the severity of the infestation.

As a simple means to visualize the infestation levels for each species over time, we assigned a value of 1 to infestations ranked low and a value of 2 to infestations ranked moderate to severe by year and state. The ranking of "low" was given when the description of the infestation was described in terms of being local, scarce, light, spotty, scattered, etc. By contrast, a ranking of "moderate to severe" was given to infestations that were described as abundant, widespread or statewide, and usually causing severe tree dieback or mortality. On a few occasions, however, a ranking of low was given to situations where infestations occurred statewide but were restricted to urban situations, such as when *A. anxius* infested primarily ornamental birch trees.

Given that populations of many native *Agrilus* species increase when host trees are weakened by various inciting factors such as drought and defoliation (Millers et al. 1989, Solomon 1995), we also recorded any mention in the reports of the possible inciting factors that could have triggered the *Agrilus* outbreaks. We recognize that changes in staffing, funding, and priorities have taken place in each DNR Forest Health Unit in the Lake States, but feel confident that the major forest pests were recorded each year and therefore the annual forest health reports represent a good approximation of changes in *Agrilus* populations over time.

Results

Agrilus anxius, *A. bilineatus*, and *A. granulatus liragus* were the only three native *Agrilus* species that were reported multiple times as forest pests in the Lake States. *Agrilus bilineatus* was reported most often in all three states, being mentioned in 90 of the 197 annual reports (16 MI, 34 MN, and 40 WI reports; Table 1). *Agrilus anxius* was the next most frequently reported species, being mentioned in 71 reports (11 MI, 33 MN, and 27 WI reports). *Agrilus granulatus liragus* was mentioned in 21 annual reports (7 MI, 11 MN, and 3 WI reports). Based on all 197 reports, *A. anxius* was first reported in 1951 in Minnesota, and *A. bilineatus* and *A. granulatus liragus* were both first reported in Wisconsin in 1966 and 1977, respectively.

Various weather-related phenomena and several defoliators were listed as suspected inciting factors that could have weakened trees and thereby led to population increases of *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* in the Lake States (Table 2). Inciting factors were presented for 72% of the 182 listings of when these three *Agrilus* species reached reportable levels (62% of the 71 *A. anxius* listings, 74% of 90 *A. bilineatus* listings, and 95% of 21 *A. granulatus liragus* listings). Drought was the most commonly reported inciting factor for all three *Agrilus* species combined (listed 119 times), as well as individually for *A. anxius* (44 times), *A.*

Table 2. Frequency (number of annual reports by state) of various inciting factors that were associated with population increases of *Agrilus anxius*, *A. bilineatus* and *A. granulatus liragus* in Michigan (MI; 66 reports during 1950–2017), Minnesota (MN; 64 reports during 1950–2017), and Wisconsin (WI; 67 reports during 1951–2017) based on each state's published annual forest health reports.

Inciting factor by *Agrilus* species (including defoliator species, family, and common name)	State		
	MI (66 yr)	MN (64 Yr)	WI (67 yr)
***Agrilus anxius,* bronze birch borer**			
Drought	10	18	16
Late spring frost	1	–	–
Hymenoptera			
Fenusa pumila Leach, Tenthredinidae, birch leafminer	–	4	1
Lepidoptera			
Bucculatrix canadensisella Chambers, Bucculatricidae, birch skeletonizer	–	1	–
Malacosoma disstria Hübner, Lasiocampidae, forest tent caterpillar	–	5	–
***Agrilus bilineatus*, twolined chestnut borer**			
Drought	16	19	23
Hail or ice storm	–	–	2
Late spring frost	–	–	2
Strong wind event	–	1	1
Orthoptera			
Dendrotettix quercus Packard, Acrididae, post–oak locust	–	–	4
Lepidoptera			
Acleris semipurpurana (Kearfott), Tortricidae, oak leaftier	–	–	2
Alsophila pometaria (Harris), Geometridae, fall cankerworm	–	3	9
Archips argyrospila (Walker), Tortricidae, fruittree leafroller	–	–	1
Archips semiferanus (Walker), Tortricidae, oak leafroller	5	–	–
Bucculatrix ainsliella Murtfeldt, Bucculatricidae, oak skeletonizer	–	–	1
Erannis tiliaria (Harris), Geometridae, linden looper	–	3	–
Lochmaeus manteo Doubleday, Notodontidae, variable oakleaf caterpillar	–	–	2
Lymantria dispar (L), Erebidae, gypsy moth	1	–	1
Malacosoma disstria Hübner, Lasiocampidae, forest tent caterpillar	2	8	6
Symmerista canicosta Franclemont, Notodontidae, redhumped oakworm	–	–	1
Symmerista leucitys Franclemont, Notodontidae, orangehumped mapleworm	–	–	1
Phasmida			
Diapheromera femorata (Say), Diapheromeridae, northern walkingstick	–	–	3
***Agrilus granulatus liragus*, bronze poplar borer**			
Drought	7	8	2
Lepidoptera			
Choristoneura conflictana (Walker), Tortricidae, large aspen tortrix	4	–	1
Malacosoma disstria Hübner, Lasiocampidae, forest tent caterpillar	4	7	1

bilineatus (58 times), and *A. granulatus liragus* (17 times; Table 2). Other weather events listed as inciting factors for population increases of these *Agrilus* (mostly for *A. bilineatus*) included late spring frosts, hail, ice storms, and strong wind events (Table 2). Several of the reports also mentioned tree age (i.e., overmaturity) as well as sandy soils and shallow soils as predisposing factors that increased tree vulnerability to *Agrilus* infestation, especially during periods of drought.

The greatest diversity of defoliators listed as inciting factors for population increases of the three *Agrilus* species was associated with *A. bilineatus* (13 defoliator species, representing 8 families in 3 orders), followed by *A. anxius* (3 defoliators in 3 families and 2 orders), and *A. granulatus liragus* (2 defoliators in 2 families in 1 order; Table 2). The top two defoliators mentioned as inciting factors for each *Agrilus* species were, in decreasing order, *Fenusa pumila* Leach [formerly *F. pusilla* (Lepeletier)] and *Malacosoma disstria* Hübner (both tied) for

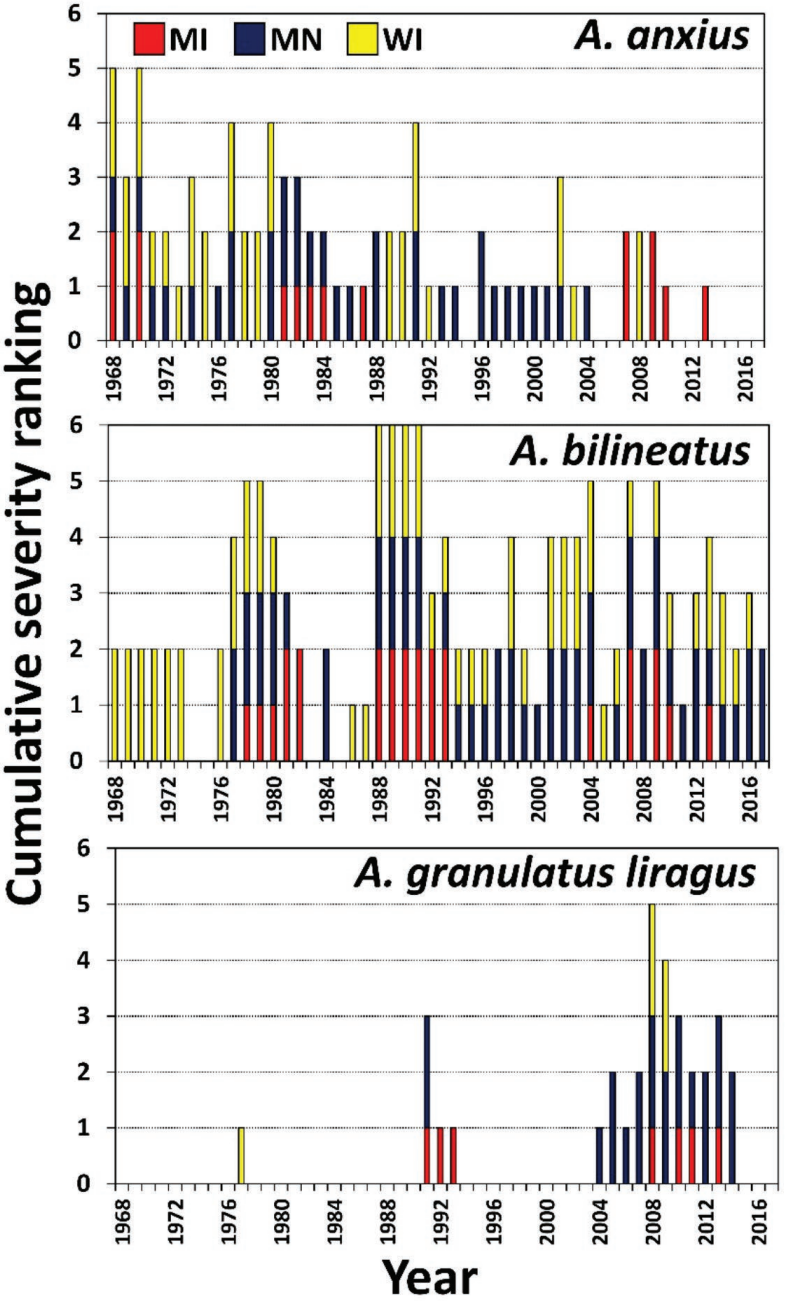

Figure 1. Stacked bar graph (within years) showing the cumulative severity rankings (0–2 for each state by year) of *Agrilus anxius*, *A. bilineatus*, and *A. granulatus liragus* infestations in Michigan, Minnesota, and Wisconsin during 1968–2017 based on annual forest pest reports from each state. A value of 0 signifies that the insect was not reported as a pest, 1 represents an infestation ranked low, and 2 represents an infestation ranked moderate to severe within each state by year. See text for more details.

A. anxius; *Alsophila pometaria* (Harris) and *M. disstria* for *A. bilineatus*; and *M. disstria* and *Choristoneura conflictana* (Walker) for *A. granulatus liragus*. The insect order, family and common name for each defoliator are listed in Table 2. *Malacosoma disstria* was the only defoliator listed as an inciting factor for all three *Agrilus* species (Table 2).

The historic timeline of *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* reaching pest status in the Lake States is depicted for the 50-year period during 1968–2017 in Fig. 1. For the years not shown in Fig. 1 (1950–1967), there were no reports for any of the three *Agrilus* species in Michigan, six reports for *A. anxius* in Minnesota (1951, 1955, 1958–59, 1961, and 1964), and eight reports for *A. anxius* (1953, 1959–62, and 1965–67) and two reports for *A. bilineatus* (1966–67) in Wisconsin. *Agrilus anxius* was reported as a pest in all three states in the same year only twice, in 1968 and 1970 (incited by drought and late frost), and only once for *A. granulatus liragus* in 2008 (incited by drought and *C. conflictana* and *M. disstria* defoliation; Fig. 1). By contrast, there were 12 years when *A. bilineatus* was reported as a pest in all three states: 1978–80, 1988–91, 1993, 2004, 2007, 2009, and 2013; usually with drought and various combinations of defoliators listed as the inciting agents (Fig. 1). Moreover, during the 3-yr period 1988–1990, *A. bilineatus* infestations were reported as moderate to severe in all three states, with drought and defoliation listed as the main inciting factors (Fig. 1).

Four additional native *Agrilus* species were mentioned in the 197 reports we reviewed and all in Wisconsin, including *A. otiosus* Say, which was reared from dying hickory (*Carya*) trees that were also infested with the bark beetle *Scolytus quadrispinosus* Say (Curculionidae: Scolytinae) and the canker fungus *Ceratocystis smalleyii* Johnson and Harrington (WI DNR 2005). The other three *Agrilus* species were *A. arcuatus* (Say), *A. cliftoni* Knull, and *A. transimpressus* Fall, all of which were reared in 2012 from dead and dying branches of declining black walnut trees (*Juglans nigra* L.) (WI DNR 2012; Andrea Diss-Torrance and Michael Hillstrom, pers. comm.). Two of these three walnut-infesting species (*A. cliftoni* and *A. transimpressus*) were recognized recently as new state records for Wisconsin (Hoftiezer 2011). Collections of the above hickory- and walnut-infesting *Agrilus* species resulted from targeted surveys of declining hickory and walnut stands in Wisconsin (WI DNR 2005, 2012).

Discussion

It is not surprising that *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* were the most commonly reported *Agrilus* species in the Lake States, given that their respective hosts, *Betula*, *Populus* and *Quercus*, are among the most common hardwood trees (i.e., broadleaf trees, dicots) in the region (MN DNR 2017, Pugh et al. 2017, WI DNR 2018), and that these three *Agrilus* species are the most damaging *Agrilus* species that infest these host trees in the Lake States (Millers et al. 1989, Solomon 1995). As background, consider that the land areas of the Lake States are heavily forested (56% of MI, 32% of MN, and 49% of WI), and that hardwood forest types dominate the forestland in each state (73% in MI, 69% in MN, and 80% in WI) (MN DNR 2017, Pugh et al. 2017, WI DNR 2018). The aspen-birch forest type is the most common forest type in Minnesota, it ranks second in Michigan and third in Wisconsin. By contrast, the oak-dominated forest types rank first in Wisconsin, second in Minnesota, and third in Michigan. The most common forest type in Michigan is the sugar maple/beech/yellow birch type (Pugh et al. 2017).

There are also many conifers (e.g., softwood trees, gymnosperms) in the Lake States, but none serve as larval hosts for any *Agrilus* species in this region (Jendek and Poláková 2014). In fact, the only *Agrilus* species worldwide to be reared from a conifer host is *A. schwerdtfegeri* Schwerdtfeger, which emerged from a dead branch of *Pinus maximinoi* Moore (= *P. tenuifolia* Bentham) in Guatemala (Jendek 2013b).

The relationship of defoliation and drought with population increases of *A. anxius*, *A. bilineatus*, and *A. granulatus liragus* in the Lake States (Table 2), has been documented for many other *Agrilus* species worldwide (Ohgushi 1978, Vansteenkiste et al. 2004, Sever et al. 2012, Sallé et al. 2014, Chamorro et al. 2015). Tree responses to defoliation and drought can be highly variable, depending on factors such as seasonality of the stress event (early summer vs. late summer), severity (mild vs. severe), and duration (one year vs. multi-year) (Kulman 1971, Kozlowski et al. 1991). Some typical early responses to defoliation include a reduction in tree carbon balance, fine root growth, and water uptake, followed by mobilization of stored reserves to develop and expand replacement foliage, which often reduces subsequent stem growth and concentrations of various defensive compounds present in stem tissues (Kulman 1971, Wright et al. 1979, Ericsson et al. 1980, Heichel and Turner 1983, Herms and Mattson 1992, Wargo 1996, Krokene 2015). Similarly, the response

of phytophagous insects to drought-stressed trees can vary widely by feeding guild, with borers usually being favored by drought (Mattson et al. 1988, Larsson 1989, Huberty and Denno 2004, Rouault et al. 2006, Haavik et al. 2015, Showalter et al. 2018). For example, severe drought can reduce a tree's ability to develop callus tissue, which can engulf and kill young wood-boring larvae such as *Agrilus* larvae (Sallé et al. 2014).

The greater frequency of *A. bilineatus* outbreaks in the Lake States as compared with *A. anxius* and *A. granulatus liragus* (Table 1, Fig. 1) may reflect differences in xylem structure of their host trees, with *A. bilineatus* infesting *Quercus* with ring-porous xylem, while *A. anxius* infests *Betula* and *A. granulatus liragus* infests *Populus*, which both have diffuse-porous xylem. This is an important difference, given that water moves primarily in the outermost annual ring of xylem in ring-porous trees, compared with several annual rings in the outermost sapwood in diffuse-porous trees (Kozlowski 1961, Wiant and Walker 1961, Kozlowski and Winget 1963). This difference also helps explain why ring-porous trees are more vulnerable to girdling insects like *Agrilus* larvae as well as pathogens that invade the outer xylem and cause wilt diseases such as chestnut blight, Dutch elm disease, and oak wilt (Zimmermann and McDonough 1978). As an example consider the study in Wisconsin by Haack and Benjamin (1982) where the current-year annual ring of xylem along the main trunk of mature red (*Q. rubra* L.) and black (*Q. velutina* Lam.) oaks measured 0.8–1.8 mm in width, whereas the average width (measured at the widest point between the dorsal and ventral surfaces of the enlarged prothorax, Chamorro et al. 2015) of third instar *A. bilineatus* larvae measured 0.9 mm and fourth (last) instars measured 1.3 mm, indicating that late-instar *A. bilineatus* larvae could easily girdle the outermost annual ring of xylem in many host trees.

Differences in xylem structure also influence the within-tree attack pattern of *Agrilus* species as well as the ease in detecting infested trees. For example, in ring-porous trees, once the xylem tissue of a portion of a branch or the trunk is completely girdled, all foliage above the girdled area usually wilts and dies that same year. For *A. bilineatus*, this usually happens in late summer when most larvae are last instars and their feeding galleries are sufficiently deep to girdle the outer annual-ring of xylem (Haack and Benjamin 1982, Haack and Acciavatti 1992). Since *A. bilineatus* females apparently lay eggs only on live portions of a host tree, the area of current-year infestation moves downward from the crown to the lower trunk in each subsequent year of attack (Haack and Benjamin 1982, Haack et al. 1983, Petrice and Haack 2014). By contrast, the first appearance of wilting foliage and dieback on birch and aspen, which have diffuse-porous xylem, usually requires multiple years of infestation by *A. anxius* and *A. granulatus liragus* before enough annual rings of the outer conducting xylem have been effectively girdled to reduce translocation and cause dieback (Barter 1957, 1965, Solomon 1995, Muilenburg and Herms 2012). Moreover, given that dieback is more gradual in birch and aspen, infestation can occur throughout the entire tree as well as in the same area of a tree for several consecutive years until that portion of the tree dies (Loerch and Cameron 1984). As an example of the difference in timing of crown dieback in response to a stress event, consider the widespread severe drought that occurred in 1988 throughout the Lake States (Trenberth et al. 1988, Haack and Mattson 1989, Jones et al. 1993), with widespread oak mortality reported in all three Lake States in 1988 and continuing through to 1991 (Fig. 1), compared with fewer and more delayed infestations reported for *A. anxius* or *A. granulatus liragus* (Fig. 1).

In recent years, most aerial surveys for forest pests in the Lake States occur in early summer, which enhances detection of current-year, early-season defoliators. However, given that foliar wilting and discoloration of *Agrilus*-infested trees usually does not occur until late summer, this practice would usually lead to an undercount of the number of areas infested with species of *Agrilus*, and therefore the outbreak history depicted in Fig. 1 should be considered as an underestimate of the actual number of *Agrilus* infestations that took place in the Lake States. Another difference between ring-porous and diffuse-porous trees that can influence the results of early-season aerial surveys is that ring-porous trees tend to leaf out later than diffuse-porous trees in any given area (Panchen et al. 2014). This occurs because in ring-porous trees, current-year earlywood xylem, which contains mostly large-diameter vessels that transport the bulk of the water, is produced before budburst, whereas in diffuse-porous trees, most current-year xylem is produced after leaf elongation (Umebayashi et al. 2008, Takahashi et al. 2013, Foster 2017).

Nonetheless, even in situations where late-summer aerial surveys are conducted, it would be easiest to detect first-season infestations of *A. bilineatus* because foliage will wilt and discolor during the first year of attack if the infested portion of the tree is completely girdled. By contrast, *Agrilus*-infested birch and aspen usually require multiple years of infestation before showing

dieback and if infestations only occur for one or two years the trees may callus-over old galleries and recover (Balch and Prebble 1940, Anderson 1944, Barter 1957, 1965). Given this situation, it is likely that *Agrilus* infestations of birch and aspen occur more often than depicted in Fig. 1.

Many species of *Agrilus*, as well as other borers, preferentially infest overmature trees, especially during periods of stress (Balch and Prebble 1940, Kozlowski 1969, Dunbar and Stephens 1976, Solomon 1995, Williams et al. 2013, Brown et al. 2015). Such a relationship, along with the forest history of the Lake States, is important to consider when viewing the pattern of *Agrilus* outbreaks depicted in Fig. 1. Consider that most of the virgin forests in the Lake States were logged during the late 1800s and early 1900s, with many large-scale forest fires soon following (Stearns 1997, Dickmann and Leefers 2003). Much of the cut-over land was soon abandoned, or farmed for short periods of time and then abandoned. Many of these degraded lands were then colonized by "pioneer" tree species, such as aspen (*P. grandidentata* Michx. and *P. tremuloides* Michx.) and paper birch (*B. papyrifera* Marshall), which are short-lived trees that reach physiological maturity at 50-70 years (Burns and Honkala 1990). Although some oaks in the Lake States are relatively short-lived (*Q. ellipsoidalis* E.J. Hill), most oaks are moderate to long-lived species (Loehle 1988, Burns and Honkala 1990, Barnes and Wagner 2004). Forest surveys conducted in the Lake States in the early 1990s indicated a skewed distribution with a large "wave" of forest stands then 55–75 years old (Stone 1997). More recent forest surveys in the Lake States (2014 for MI, 2016 for MN, and 2015 for WI) indicate sharp reductions in aspen and birch acreage, especially in older age classes, compared with increases in acreage of oak-dominated forests, especially in older age classes (Pugh et al. 2017, MN DNR 2017, WI DNR 2018). Such shifts in the species composition and age structure of forests in the Lake States may explain, in part, the decline in *A. anxius* outbreaks in recent years, the recent spike in the early 2000s of *A. granulatus liragus* activity, and the near steady activity of *A. bilineatus* over the past several decades (Fig. 1).

The defoliators listed in Table 2 are common throughout the Lake States as well as in much of eastern North America, and a few also occur in the West (e.g., *C. conflictana*, *F. pumila*, and *M. disstria*; Drooz 1985). At times, outbreaks of *C. conflictana* and *M. disstria* cover millions of hectares and can continue for multiple years before subsiding (Prentice 1955, Drooz 1985, Ciesla and Kruse 2009, Schowalter 2017). Of the defoliators listed in Table 2, only two are exotic to North America (*F. pumila* and *Lymantria dispar* (Linnaeus)), and both are far less outbreak prone today than in the past as a result of introduced natural enemies: mostly parasitoids for *F. pumila* (Kirichenko et al. 2019), and a fungus and virus for *L. dispar* (Solter and Hajek 2009). In addition, all of the defoliators listed in Table 2 initiate larval feeding in early summer, with the exception of the two *Symmerista* species, which are late-season defoliators (Drooz 1985). Early-season defoliation typically reduces same-year tree growth more than late-season defoliation because trees often use stored reserves to refoliate after early-season defoliation, but seldom refoliate after late-season defoliation (Kulman 1971, Ericsson et al. 1980). However, severe late-season defoliation can have a greater impact on stem growth the following year, compared with early season defoliation (Mattson et al. 1988). With respect to *Agrilus* adult activity, early-season defoliation would usually occur prior to peak *Agrilus* oviposition, whereas late-season defoliation would usually occur after most *Agrilus* oviposition had ended for the year. Outbreaks of many defoliators are also favored during periods of drought (Mattson and Haack 1987, Millers et al. 1989), and drought plus defoliation would likely even more significantly weaken trees, which would further increase tree susceptibility to borer infestation (Thomas et al. 2002).

Now that *A. bilineatus* has become established in Turkey (Hızal and Arslangündoğdu 2018, EPPO 2019a), it is difficult to predict how damaging this species will be to European chestnut and oak trees. Drought and widespread defoliation of hardwood trees are also common in Europe (Gibbs and Greiggi 1997, Moraal and Hilszczanski 2000, Thomas et al. 2002, Sallé et al. 2014, Tiberi et al. 2016) and will likely make European host trees susceptible to *A. bilineatus* attack. However, throughout Europe there are several native species of *Agrilus* that utilize chestnut and oak trees as larval hosts (Jendek and Poláková 2014). Among these, *A. biguttatus* Fabricius is considered the most destructive, especially on oaks, which also commonly reaches outbreak levels in response to defoliation and drought (Moraal and Hilszczanski 2000, Sallé et al. 2014). Therefore, if European host trees are not highly susceptible to *A. bilineatus*, then *A. bilineatus* will likely encounter high levels of competition from native European *Agrilus* for hosts and consequently *A. bilineatus* may only become a minor pest in Europe. On the other hand, if some European chestnut and oak species are highly susceptible to *A. bilineatus* infestation, such as was the case when European *Quercus robur* L. trees were

planted in Michigan (Haack 1986, Haack and Petrice 2020), then *A. bilineatus* could become a major pest in Europe. Nonetheless, given that drought is predicted to increase in frequency and severity in the future, outbreaks of *Agrilus* species and many other forest insects are expected to become more common in the United States and worldwide (Allen et al. 2010, Kolb et al. 2016).

Acknowledgments

The authors thank the many forest health staff of the Departments of Natural Resources in Michigan, Minnesota, and Wisconsin for preparing the annual forest pest reports for the past several decades; Val Cervenka for supplying many of the early Minnesota forest pest reports; Andrea Diss-Torrance, Michael Hillstrom, Eduard Jendek, and Daniel Young for providing personal communications and unpublished data, and Daniel Herms, Brian Schwingle, Richard Westcott and two anonymous reviewers for commenting on an earlier version of this paper.

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Use of Nest and Pollen Resources by Leafcutter Bees, Genus *Megachile* (Hymenoptera: Megachilidae) in Central Michigan

Killewald, M. F.[1,2] *, L. M. Rowe[1,3], K. K. Graham[1], T. J. Wood[1,4], and R. Isaacs[1]
[1] Department of Entomology, Michigan State University, East Lansing, MI 48824
[2] Department of Entomology, University of Manitoba, Winnipeg, MB R3T 2N2
[3] Michigan Natural Features Inventory, 525 W. Allegan Street, Lansing, MI 48933
[4] Laboratory of Zoology, University of Mons, 700, Mons, Belgium
*Corresponding author: (e-mail: killewam@myumanitoba.ca) (204) 474-7485

Abstract

Many landscapes throughout the Great Lakes region have experienced reductions in floral and nesting resources for bees. Identifying the resources used by bees in the family Megachilidae can be used to inform conservation programs that aim to support this group. In this study, we identified the preferred nesting substrate and size, as well as the proportion of distinct pollen types used for offspring provisioning by *Megachile* (Hymenoptera: Megachilidae) species. A total of 39 completed artificial nesting tubes were collected between July 25 and August 30, 2016. A majority of completed nests were in 4 mm diameter tubes. However, more 6 mm and 7 mm diameter nests were occupied later in the season. A total of 98 cells from 20 nests were analyzed for the composition of the pollen provisions. Nesting females gathered pollen primarily from *Trifolium repens* L.-type (70.2% of total pollen) and the majority of collection of this species occurred between July 25 and August 10. There was also frequent pollen collection from *Centaurea stoebe* (L.) (9.0%), *Rudbeckia*-type (8.4%), and *Cirsium* spp. (8.3%) with the majority of collection from these species occurring after August 10. Our results show that *Megachile* species at our mid-Michigan site exhibited strong preferences for specific nest hole sizes, and they primarily collected pollen from non-native plants. This information can inform efforts to build local populations of these summer-active bees using combined nesting and foraging resources.

Keywords: Pollen identification, pollinator, bee, stem, nest

Leafcutter bees (Hymenoptera: Megachilidae) are important pollinators of alfalfa (*Medicago sativa* L.), clover (*Trifolium* spp.), cranberry (*Vaccinium macrocarpon* Aiton), sunflower (*Helianthus* spp.), and many wildflower species (Hobbs and Lilly 1954, Stephen and Osgood 1965b, Osgood 1974, Tepedino and Frohlich 1982, Cane et al. 1996, Pitts-Singer and Cane 2011, Richards 2015). In the wild, *Megachile* are highly adaptive, utilizing a wide range of nesting materials, including plant stems, soil, and logs, as well as man-made structures (Hobbs and Lilly 1954). Because of this plasticity, there has been increasing interest in managing these species near cropland to bolster pollination services. To manage *Megachile* species, artificial cavities of various sizes can be placed around croplands to encourage nesting. However, regionally specific information on nesting and floral resources used by different species of *Megachile* is needed to optimize efforts to increase local abundances of this genus.

Most *Megachile* use leaf material to make their nests in decaying logs or inside the hollow stems of plants, but some species make their nests underground (Hobbs and Lilly 1954, Gibbs et al. 2017). The inner walls of the nest are lined with cut leaf material to form a cell (Frolich and Parker 1983), with some species using masticated leaf material and soil (Medler 1964). They then provision this cell with pollen and nectar before laying an egg and finally sealing the cell with more leaf material (Ivanochko 1979). This process is repeated several times from the back to the front of the cavity until it is full of completed cells. Once the nest is full of completed cells, an endcap of leaf material is added to protect their offspring. Once the endcap is added, the nest is now completed and the female begins another (Frolich and Parker 1983, Peterson and Artz 2014). Within the Great Lakes region, the natural nesting biology of several species of *Megachile* is well studied, and we can use this foundation to inform selection of nesting materials for management (Medler and Koerber 1958, Medler

1959, 1964, Medler and Lussenhop 1968). Nesting habits of some commonly managed *Megachile*, such as *M. rotundata* (Fabricus), may vary significantly, as they are known to nest in cavities with diameters as variable as 3–4 mm (O'Neill et al. 2010) to 6–7 mm in diameter (Stephen and Osgood 1965a). But we still know relatively little about the optimal nesting materials that should be provided to bolster local populations of *Megachile* in general (instead of targeting specific species). Clarifying the optimal materials and sizes to provide *Megachile* species in the Great Lakes region will therefore optimize efforts by growers and conservationists to increase local populations.

Similarly, the floral resources used by *Megachile* species in the Great Lakes region are not well studied, and a better understanding of resource use could aid in increasing local abundance of *Megachile*. Although lists of visited plants for different *Megachile* species exist (Ascher and Pickering 2019), there is little information on which plants this genus uses for pollen foraging specifically, as these plant associations are often more restrictive than those plants visited for nectar (Williams 2003). It has been shown that some *Megachile* species often provision nests with pollen from a restricted number of plant species, such as Asteraceae or Fabaceae species (Tepedino and Frohlich 1982, O'Neill et al. 2004), and that this number of plant species may be further restricted when factors such as intensive agriculture reduce floral abundance and diversity in the area (Rich and Woodruff 1996). Pollen resources are critical for brood development (Nelson et al. 1972), and clarifying the pollen provisioning behavior of this group of bees is needed to better understand their resource requirements.

Pollen analysis can be used to identify dietary preferences and host-species fidelity in bees (Beil et al. 2008). Most traditional collection methods revolve around hours of searching for individual bees in the field. However, pollen analysis of trap nests allows researchers to passively monitor the diet of cavity nesting bees with minimal time spent in the field and removes floral associations that are used for nectaring only. Given that pollen provisioning preferences of *Megachile* species are not well studied in the Great Lakes region, understanding the pollen use and nesting preferences of this group is important for their management.

At a site in central Michigan where multiple native wildflower species were established to evaluate their use by bees (Rowe et al. 2018), we addressed the following questions: 1) What nest diameters are utilized by the *Megachile* species at this site? and 2) What are the primary pollen species collected by these bees?

Methods

Study site. This research was conducted during the summer of 2016 at the Clarksville Research Center (CRC) located near Clarksville, MI (42.873390, -85.258496). Fifty-three native wildflower species (S1) were established in individual plots replicated four times, across a three-acre area (Rowe et al. 2018). Within a 1 km radius of the study site, the landscape was dominated by non-rewarding agricultural land (54.1%), but also included 20.3% of rewarding agricultural land, 10.4% forests, 7.3% of developed land, 3.5% wetlands, 3.2% fallow agricultural land, and 0.7% other classification types (Fig. 1). Non-rewarding agricultural land is comprised of crops that do not produce resources that are generally used by bees. Corn, oats, rye and sorghum are included in the non-rewarding agricultural land category. Similarly, rewarding agricultural land is comprised of crops that produce resources generally used by bees, such as alfalfa, cucumbers, clover, wildflowers, and apples. These data were extracted from the Crop Data Layer (USDA National Agricultural Statistics Service Cropland Data Layer 2016) with 30 m spatial resolution using ArcGIS 10.2.2 (ESRI 2014). Full details of the site layout, plant species used, and experimental design can be found in Rowe et al. (2018).

Nest boxes. To identify preferences for nest tube diameter and material, four nesting boxes containing a variety of materials were placed at CRC in May 2016 (Fig. 2). Each nest box was made from a plastic mail tote (Uline, Pleasant Prairie, WI) that was 18 x 13 x 12" in size and contained four sizes of cardboard nesting tube (4, 5, 6, and 7 mm inside diameter) in bundles of 62 nests (Jonesville Paper Tube Company, Jonesville, MI), a reusable wooden nest tray with 8 mm inside nest diameter containing a total of 72 available holes (Crown Bees, Woodinville, WA), and a cluster of 12 pieces of bamboo with hole diameters ranging from 8–16 mm. Nests were secured inside the nesting box with a piece of 2 x 3" wood oriented vertically and zip ties holding the nesting substrate to the wood. During the summer of 2015, only four *Megachile* were collected during the season long bee surveys carried out by Rowe et al. (2018). To encourage nesting, 131 overwintering *Megachile* cocoons were placed in each nesting box in early May. Most of the released cocoons were of *M. rotundata*, but other overwintering *Megachile* species could have been released as well since most unopened *Megachile* cocoons can-

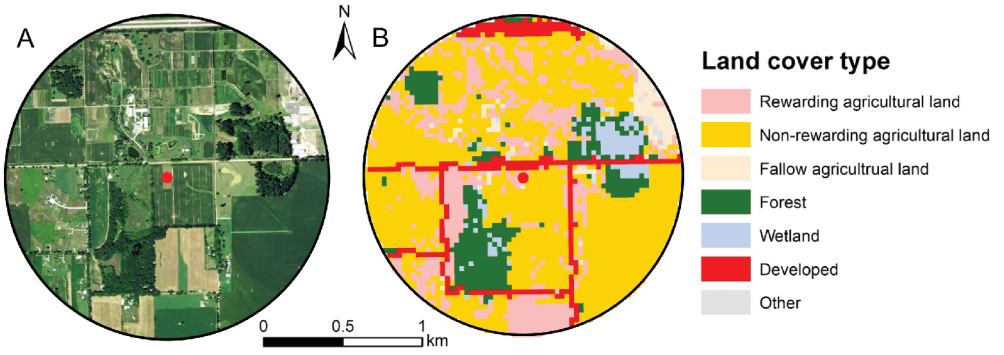

Figure 1. A. An aerial image with a 1km radius around the Clarksville Research Station (CRC) with a 1m resolution. B. An aerial view of the site with different landscape classifications. The image was extracted from Crop Data Layer (USDA National Agricultural Statistics Service Cropland Data Layer 2016) with 30 m spatial resolution using ArcGIS 10.2.2 (ESRI, 2014).

not be identified to species. Of the released cocoons at each nesting box, 44% were 4mm, 47% were 6–8 mm, and 10% were 8–10 mm. These cocoons were originally collected from nests in a native bee hotel at Michigan State University, in which *M. rotundata* and *M. pugnata* (Say) were commonly observed nesting (Gibbs et al. 2017).

Nest sampling. Nest boxes were checked weekly from May until September for completed nests, which were removed and replaced with new nests to maintain a consistent number of available cavities throughout

Figure 2. One of the four nest boxes placed at the Clarksville Research Center (CRC) in the summer of 2016. Artificial nesting material inside the box includes four sizes of cardboard nests (4, 5, 6, and 7 mm inside diameter), a reusable wood block (8 mm inside diameter), and 12 bamboo nests with varying diameters from 8-20 mm.

the season. *Megachile* nests were assigned a week category based on the collection date so trends in nesting and pollen could be visualized. Week one marked the first completed nest and week 4 marked the end of nesting. A week was considered Monday–Sunday, with July 25, August 1, August 8, August 15, 2016 marking the beginning of weeks 1–4, respectively. All collected nests were placed into a –23°C freezer within 2 hours after collection to terminate larval development.

Analysis of pollen from nests. Pollen was isolated by removing plant material and placing the pollen ball into a 1.5 mL centrifuge tube. These samples were then stored in a –23°C freezer before further processing. For each week of nesting, alternating cells were analyzed for five nests. To better visualize features of the pollen grains, some selected samples were processed using acetolysis according to Louveaux et al. (1978) and Jones (2014). The remaining samples that were not processed with acetolysis were processed according to Westrich and Schmidt (1986). Samples were diluted with 70% ethanol, vortexed, and immediately a subsample was pipetted onto a microscope slide. A piece of fuschin gel was heated and then a cover slip was added to the center of each pollen sample (Westrich and Schmidt 1986). Amounts of ethanol were varied to keep a consistent amount of pollen on the microscope slides for identification, ranging from 250 µl to 1 mL, with full pollen loads receiving 1 mL of ethanol and minimal pollen loads receiving 250 µl.

For both processing methods, volumes of pollen species were visually estimated (Folk 1951) for each pollen load. Pollen species were identified to the lowest taxonomic rank using Sawyer (1981) and a reference collection that was processed using similar methods. Pollen slides processed with acetolysis were identified using a reference collection that was also processed with acetolysis. Likewise, non-acetolysized samples were only compared to a non-acetolysized reference sample. For the non-acetolysized samples, pollen species were identified against a reference collection of 254 plant species collected across Michigan. The acetolysized samples were compared to a reference collection of 73 plant species collected across Michigan. Pictures of pollen species from both reference collections are available online (https://www.flickr.com/photos/161453633@N02/collections). If the identity of the pollen species was not certain, similar pollen grains were lumped into type categories or lowest taxonomic level possible. Reference collections included plants established in the wildflower planting (Rowe et al. 2018).

Results

A total of 39 completed *Megachile* nests were collected during the sampling period between July 25 and August 15, 2016 (Fig. 3). The *Megachile* at our site nested more frequently in 4 mm nests than any other diameter, with almost 50% of the nesting in this tube size. However, later in the nesting season, after August 10, more 6 mm and 7 mm nests were utilized than 4 mm nests. No *Megachile* nests were found in the 5mm cardboard tubes or the wooden nesting block, and only 6 completed bamboo nests were collected at the site. The total number of completed nests of each size are summarized in Table 1.

Half of the collected nests were randomly selected for pollen analysis, totaling 98 cells from 20 nests. Pollen analysis identified seven distinct pollen types: *Trifolium repens* L.-type, *Centaurea stoebe* (Linnaeus), *Rudbeckia*-type, *Cirsium* spp., *Trifolium pretense* L., Unknown pollen, and *Lotus corniculatus* (Linnaeus). Over the entire nesting season, *Megachile* species primarily collected *T. repens*-type (70.2%), *C. stoebe* (8.9%), *Rudbeckia*-type (8.4%), and *Cirsium* pollen (8.3%). All other pollen types were present in < 3% abundance. Most of the pollen species identified from nests were not collected from the sown plant species. However, *Rudbeckia*-type pollen could be a sown species, with only 4 sown species having a similar pollen structure. Similarly, *C. stoebe* and *L. corniculatus* were sown, but

Table 1. Number of nests of each size completed by *Megachile* spp. at the Clarksville Research Center during 2016.

Nesting substrate (inside diameter)	Total nests completed	Percent of total nests
Paper tube (4 mm)	20	48.8
Paper tube (5 mm)	0	0
Paper tube (6 mm)	9	22.0
Paper tube (7 mm)	6	14.6
Wood block (8 mm)	0	0
Bamboo (8-10 mm)	6	14.6

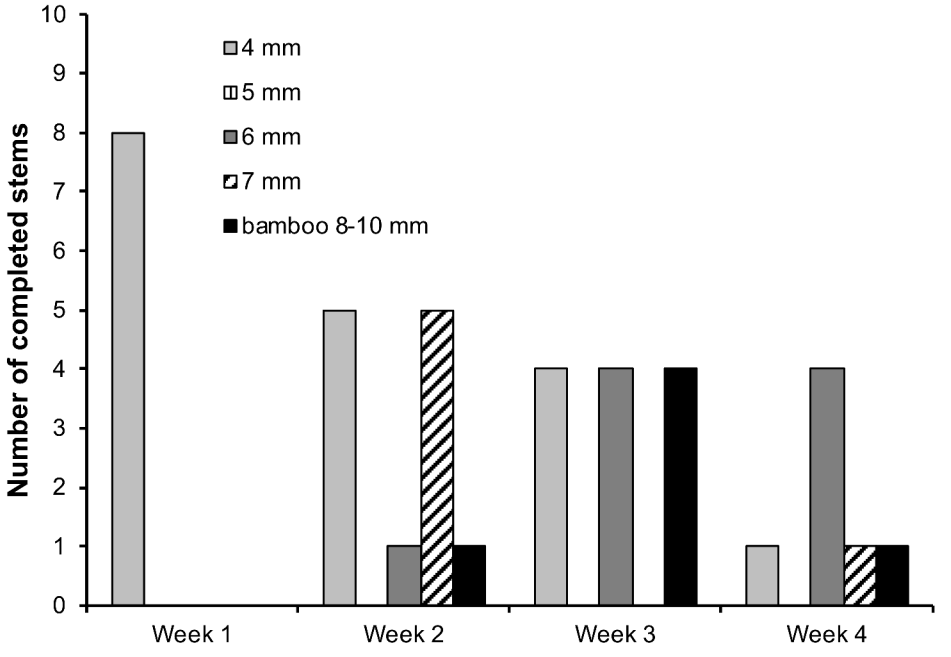

Figure 3. The number of completed nests collected per week at the Clarksville Research Center (CRC) during the summer of 2016.

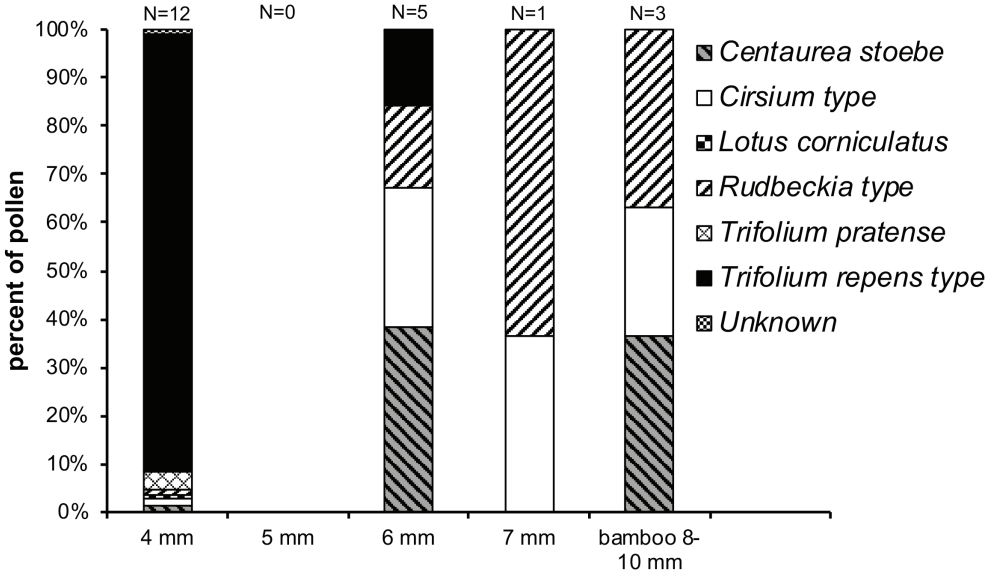

Figure 4. Pollen composition of each nest size. Nests were collected at the Clarksville Research Center during the summer of 2016.

Table 2. Identified pollen groups with their taxonomic constituents from *Megachile* nests collected at the Clarksville Research Center during 2016.

pollen type	order	Family	genus	species
Lotus corniculatus	Fabales	Fabaceae	*Lotus*	*corniculatus*
Trifolium pratense	Fabales	Fabaceae	*Trifolium*	*pratense*
Trifolium repens-type	Fabales	Fabaceae	*Trifolium*	
			Medicago	
			Melilotus	
Centaurea stoebe	Asterales	Asteraceae	*Centaurea*	*stoebe*
Cirsium	Asterales	Asteraceae	*Cirsium*	
Rudbeckia-type	Asterales	Asteraceae	*Rudbeckia*	
			Coreopsis	
			Echinacea	
			Ratibida	

there was also an abundance of these species in the surrounding landscape. A summary of pollen composition of each nest size is available in Fig. 4.

The pollen species utilized by nesting *Megachile* varied throughout the season. *Megachile* species used Fabaceae pollen almost exclusively (100% in week 1 and 81.6% in week 2) early in the nesting season. However, in weeks 3 and 4, *Megachile* species utilized more Asteraceae pollen than in previous weeks. Abundances of Fabaceae pollen (*T. repens*-type, *T. pratense*, and *L. corniculatus*) decreased over time from 100% in week 1, to 81.6% in week 2, to 29.8% in week 3, and finally increased slightly in week 4 to 62.1%. This trend was mostly driven by *T. repens*-type. The abundance of *T. repens*-type declined from 95.8% in week 1 to 29.7% in week 3, but increased slightly to 57.1% in week 4. Abundances of Asteraceae pollen (*Cirsium*, *Rudbeckia*-type, and *C. stoebe*) increased from 18% in week 2, to 68.2% in week 3, and finally decreased to 36.4% in week 4. Pollen constituents for the type pollens are included in Table 2. A figure of pollen composition by stem size and week is available in Fig. 5.

Discussion

We found that the *Megachile* species at our site used mostly 4 mm nests early in the season (week 1) and then utilized mostly larger nests (>6 mm) later in the season (weeks 3 and 4). We also found that the

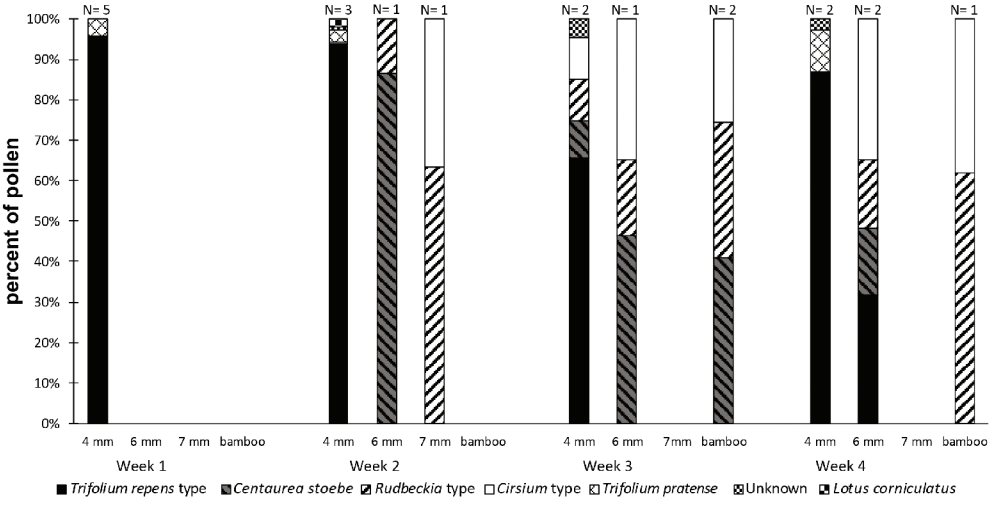

Figure 5. Pollen composition of each cavity size separated by weeks of nesting. Nests were collected at the Clarksville Research Center during the summer of 2016.

Table 3. Species of *Megachile* that were collected at the Clarksville Research Center during the summer of 2016 from the Rowe et al. (2018) study. Intertegular distance is averaged from 3 specimens collected at the site. If 3 specimens were not collected, then other specimens collected in Michigan's Lower Peninsula were measured. Standard error is given in parenthesis to the right of the average intertegular distance.

species	number collected	average intertegular distance mm	known nest size	flight time	floral preference	floral records	other info	citation
M. rotundata	8	2.44 (0.03)	4–7mm	July 20–August 8	Generalist but forages mainly on Fabaceae	*Asclepias verticillata, Lotus corniculatus, Pycanthemum virginiatum*	actively managed for alfalfa pollination, Common in MSU trap nests	Stephen and Osgood, 1965a, Gerber and Klostermeyer, 1972, Pits-Singer and Cane, 2011, Gibbs et al., 2017
M. pugnata	3	2.69 (0.09)	7–9mm	July 7–August 22	Asteraceae	*Coreopsis palmata, Echinacea purpurea*	uses masticated rather than cut leaf material for nest construction. Common in MSU trap nests	Medler, 1964, Tepedino and Frohlich, 1982, Frolich and Parker, 1983, Gibbs et al. 2017
M. frugalis	2	2.69 (0.08)	unknown	July 7–August 3	Generalist	*Asclepias tuberosa, Verbena stricta*	limited information available, Gibbs et al., 2017 only lists county records in Michigan	Rowe et al. 2018, Ascher and Pickering, 2019
M. mucida	2	3.41 (0.07)	8mm	June-16	Generalist but floral visitation records limited	*Penstemon digitalis*	emergence among the earliest of the *Megachile* species in Michigan, ground nesting	Gibbs, 2017, Gibbs et al. 2017
M. brevis	1	2.74 (0.04)	8-9mm	August-16	Generalist but forages on more Asteraceae than other families	*Rhus copallinum*	one study (Michender, 1953) found a female to nest inside a 9 mm rubber tube placed on the ground	Michener, 1953, Medler and Lussenhop, 1968
M. mendica	1	3.20 (0.07)	6.4–12.7mm	June-16	Generalist but forages on more Asteraceae than other families	*Lotus corniculatus*	nests in soil, but will accept trap nests. Krombein (1967) found one nest of this species inside a cavity 4.8 mm inside diameter, but it appears that use of nests this size are rare.	Krombein, 1967, Baker et al. 1985

Megachile at the study site primarily forage from *T. repens*-type (Fabaceae family) pollen early in the nesting season (weeks 1 and 2), but then use a mix of Asteraceae pollen later in the nesting season (weeks 3 and 4). For areas where *Megachile* species are managed for pollination services of specific crops, managers can use this information to inform their nest material and plant selection.

A shift in nesting resources and pollen preference likely indicates that different species are utilizing different resources. Seven species of *Megachile* were recorded at this site during the same growing season (Rowe et al. 2018), with *M. rotundata* being the most dominant species and *M. pugnata* being the second most common (Table 3). *Megachile rotundata* tend to nest in 4 mm inside diameter tubes (Klostermeyer and Gerber 1969), but will accept tubes ranging from 4–7 mm (Stephen and Osgood 1965a). Although this species will visit a wide range of flowers, it tends to forage on Fabaceae, especially members of *Medicago, Melilotus*, and *Trifolium* (O'Neill et al. 2004, Pitts-Singer and Cane 2011, Ascher and Pickering 2019). *Megachile rotundata* is the smallest *Megachile* species found at the site, and the only species found to use 4 mm nests (O'Neill et al. 2010). *Megachile rotundata* is also common within the nests at MSU that our nesting boxes were seeded with (Gibbs et al. 2017). Given the pollen foraging habits, local abundance, and willingness to use smaller cavities, *M. rotundata* is the most likely occupant of the 4 mm nests found at our site.

The second most common species at the site, *M. pugnata,* will nest in 7 mm inside diameter tubes (Tepedino and Frohlich 1982), but will use a range of tube sizes from 7–9 mm (Medler 1964, Frolich and Parker 1983). *Megachile pugnata* is common in both Michigan's Lower Peninsula and the MSU trap nests that the nesting boxes were seeded with (Gibbs et al. 2017). *Megachile pugnata* displays stronger pollen preferences than *M. rotundata*. One study found that *M. pugnata* uses almost exclusively Asteraceae pollen, with only 0.6 to 2.5% of collected pollen not belonging to this family (Tepedino and Frohlich 1982). The use of larger diameter cavities, preference of Asteraceae pollen, and local abundance makes *M. pugnata* a likely occupant of the larger nest sizes.

Two specimens of both *Megachile frugalis* (Cresson) and *Megachile mucida* (Cresson) were also collected at the site during the summer of 2016. Little information is known about these species, but given floral records (Ascher and Pickering 2019), both species appear to visit a wide range of flowers. It is unknown what sizes of cavities *M. frugalis* will utilize. *Megachile mucida* is found to nest in the ground (Gibbs 2017), and is quite common in mid-Michigan. The emergence of *M. mucida* is among the earliest of the Megachile species found in Michigan. Given the ground nesting behavior of *M. mucida*, it is likely not a candidate for the larger diameter stems collected at our site.

Two other species of *Megachile*, *M. brevis* (Say) and *M. mendica* (Cresson), were also found at the site in 2016, but only one specimen of each species was collected. The biology of *Megachile brevis* is well documented in Kansas by Michener (1953). However, it's nesting preferences are not well known, as he did not document the nest diameters used by this species, other than a single female accepted a 9 mm rubber tube when placed on the ground. The nesting biology of *Megachile mendica* is summarized in Baker et al. (1985), where they found that *M. mendica* accepted trap nests ranging from 6.4- 9.5 mm, but a majority of nests were 8 mm inside diameter. Given floral visitation data, it appears that both *M. brevis* and *M. mendica* are generalists. However, both species show more floral associations within the Asteraceae family than other families (Ascher and Pickering 2019).

The exact identity of the nest occupants cannot be known for certain, but given floral visitation data and previous nesting studies, we believe that the occupants of the 4 mm nests were *M. rotundata*. The occupants of the larger diameters of nests are less clear, but is most likely *M. pugnata* given their abundance and oligolecty on Asteraceae pollen. *Megachile mucida* is not a likely candidate for the larger diameter stems due to its ground nesting behavior. However, it is not clear whether this species would accept artificial cavities given the option. Although the other nesting species cannot be discredited completely, they are much less common and more general in their foraging preferences that *M. pugnata.*

Our findings also suggest that nesting *Megachile* species did not utilize the majority of sown wildflowers. However, due to the difficulty of pollen identification and lack of published keys, some pollen species had to be lumped into a type category. For instance, *T. repens*-type pollen could be from a number of Fabaceae species; though, there were no Fabaceae species with *T. repens*-type pollen in the wildflower planting at our site. However, *Melilotus* and *Medicago* have a similar pollen structure to *T. repens*-type and are often lumped together (Sawyer 1981). Both of these genera were not sown, but were found within 100 m of the nest boxes, and could be possible sources of *T. repens*-type pollen. Similarly, *Rudbeckia*-type pollen could also be another Asteraceae pollen other than

Rudbeckia, and there were planted members of the Asteraceae family with a similar pollen structure in bloom during the nesting season: *Coreopsis palmata* (Nutt.), *Echinacea purpurea* (L.), *Ratibida pinnata* (Vent.), and *Rudbeckia hirta* (L.). It is therefore possible that *Rudbeckia* type pollen found in nests were from the planted species; however, overall collection of *Rudbeckia* type pollen was low.

The non-sown resources are likely more effective at local recruitment and retention of *Megachile* due to their preferences for them. Unfortunately, since some of the pollen species had to be grouped together, we cannot be certain which pollen species were the most useful. Given that many of the collected pollen species are weedy and widespread, lack of pollen resources may not be a large concern for *Megachile* in this region.

Acknowledgments

We thank Katie Boyd-Lee for her help in processing samples, Yajun Zhang for her help with landscape analysis, and Marisol Quintanilla for the use of her microscope to collect images of pollen. We thank Jordan Guy, Gabriela Quinlan, Meghan Milbrath, Steven Van Timmeren, Jacquelyn Albert, and Philip Fanning for their comments while preparing the manuscript. We thank the CRC station manager Jerry Skeltis and his staff for maintaining the research plots. This study was funded by the MSU Undergraduate Research Program (URP) and the Jeffrey Boettcher fund.

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S1. List of the sown plant species at the Clarksville Research Center. Pollen type refers to the morphological group that each plant species would be placed into based on their pollen structure.

plant species	plant family	pollen type	bloom time relative to nest construction
Lotus corniculatus	Fabaceae	*Lotus* sp.	during
Oenothera fruticosa	Onagraceae	*Oenothera* sp.	during
Achillea millefolium	Asteraceae	*Aster* type	during
Asclepias syriaca	Asclepiadaceae	*Asclepias* sp.	during
Ceanothus americanus	Rhamnaceae	*Ceanothus* sp.	during
Asclepias tuberosa	Asclepiadaceae	*Asclepias* sp.	during
Potentilla arguta	Rosaceae	*Potentilla* sp.	during
Rudbeckia hirta	Asteraceae	*Rudbeckia* type	during
Campanula rotundifolia	Campanulaceae	*Campanula* sp.	during
Amorpha canescens	Fabaceae	*Amorpha* sp.	during
Coreopsis palmata	Asteraceae	*Rudbeckia* type	during
Hypericum prolificum	Clusiaceae	*Hypericum* sp.	during
Monarda fistulosa	Lamiaceae	*Monarda* sp.	during
Hieracium gronovii	Asteraceae	*Taraxacum* type	during
Pycnanthemum virginianum	Lamiaceae	*Pycanthemum* sp.	during
Verbena stricta	Verbenaceae	*Verbena* sp.	during
Chamerion angustifolium	Onagraceae	*Chamerion* sp.	during
Centaurea stoebe micranthos	Asteraceae	*Centaurea* type	during
Solidago nemoralis	Asteraceae	*Aster* type	during
Asclepias verticillata	Asclepiadaceae	*Asclepias* sp.	during
Dalea purpurea	Fabaceae	*Dalea* sp.	during
Ratibida pinnata	Asteraceae	*Rudbeckia* type	during
Pycnanthemum pilosum	Lamiaceae	*Pycanthemum* sp.	during
Liatris cylindracea	Asteraceae	*Rudbeckia* type	during
Echinacea purpurea	Asteraceae	*Rudbeckia* type	during
Eryngium yuccifolium	Apiaceae	*Eryngium* sp.	during
Monarda punctata	Lamiaceae	*Monarda* sp.	during
Helianthus occidentalis	Asteraceae	*Helianthus* type	during
Solidago juncea	Asteraceae	*Rudbeckia* type	during
Silphium integrifolium	Asteraceae	*Helianthus* type	during
Silphium terebinthinaceum	Asteraceae	*Helianthus* type	during
Rhus copallinum	Anacardiaceae	*Rhus* sp.	during
Lespedeza hirta	Fabaceae	*Lespedeza* sp.	during
Lespedeza capitata	Fabaceae	*Lespedeza* sp.	during
Coreopsis tripteris	Asteraceae	*Rudbeckia* type	during
Packera obovata	Asteraceae	*Aster* type	before
Potentilla simplex	Rosaceae	*Potentilla* sp.	before
Lupinus perennis	Fabaceae	*Lupinus* sp.	before
Penstemon hirsutus	Plantaginaceae	*Penstemon* sp.	before
Heuchera richardsonii	Saxifragaceae	*Heuchera* sp.	before
Coreopsis lanceolata	Asteraceae	*Rudbeckia* type	before
Tradescantia ohiensis	Commelinaceae	*Tradescantia* sp.	before
Baptisia alba var. *macrophylla*	Fabaceae	*Baptisia* sp.	before
Penstemon digitalis	Plantaginaceae	*Penstemon* sp.	before
Rosa carolina	Rosaceae	*Rosa* sp.	before
Dasiphora fruticosa	Rosaceae	*Dasiphora* sp.	after
Helianthus strumosus	Asteraceae	*Helianthus* type	after
Liatris aspera	Asteraceae	*Rudbeckia* type	after
Oenothera biennis	Onagraceae	*Oenothera* sp.	after
Oligoneuron rigidum	Asteraceae	*Aster* type	after
Symphyotrichum sericeum	Asteraceae	*Aster* type	after
Symphyotrichum oolentangiense	Asteraceae	*Aster* type	after
Solidago speciosa	Asteraceae	*Rudbeckia* type	after

A Five-Year Study of the Flying Beetles (Coleoptera) from a Grassland and an Adjacent Woods in Southern Québec (Canada)

Claire Levesque[1,*] and Gilles-Yvon Levesque[1]
[1] 291 rue des Diamants, Sherbrooke, Qc, Canada J1G 4A1
*Corresponding author (e-mail: clevesque1@videotron.ca)

Abstract

During the entire snow-free season (April or May to October) in 2006-2010, we collected with four flight interception traps a total of 34629 individuals of 848 Coleoptera species belonging to 60 families in southern Québec (Canada). We caught mainly phytophagous and zoophagous beetles. The majority of species (621 or 73.2%) were represented by less than 10 adults over the five years; however, we collected at least 100 adults for 48 species, including four major species: *Meligethes nigrescens* Stephens (15.9% of the total catches), *Longitarsus luridus* (Scopoli) (10.6%), *Eusphalerum pothos* (Mannerheim) (9.1%) and *Acidota subcarinata* Erichson (5.9%). Between 39 and 47% of species from a trap were collected in one month only over the five years; whereas *E. pothos* and *M. nigrescens* flew mainly in May and June, and adults of *A. subcarinata* and *L. luridus* were collected mainly in September and October. Over 2006–2010, we caught a total of 9214 individuals of 439 species in the grassland, 7503 individuals of 519 species at the woods edge, 5943 individuals of 356 species in the woods, and 11969 individuals of 468 species near a ditch parallel to the woods. We consider that the curve of the cumulative number of species for each trap over 33 months in five years may indicate a good estimation of the flying beetle species richness in a site. Seven species were dominant in at least one trap over 2006–2010: *A. subcarinata, Bradycellus nigrinus* (Dejean), *Cercyon assecla* Smetana, *E. pothos, Isochnus rufipes* (LeConte), *L. luridus* and *M. nigrescens*. In a window trap, some dominant and subdominant species showed considerable fluctuation in percentage from year to year, particularly *E. pothos, L. luridus* and *M. nigrescens*. Also, we believe that, in the future, it will be important to explore variations of beetle biodiversity on long time.

Keywords: Coleoptera, flight interception trap, Québec.

The number of described beetle species on Earth is near 387 000 (Bouchard et al. 2017). To date, 8302 species of Coleoptera have been recorded in Canada (Brunke et al. 2019). The four most diverse families of beetles in Canada are the Staphylinidae (1774 spp.), Carabidae (983 spp.), Curculionidae (826 spp.) and Chrysomelidae (595 spp.). A total of 639 non-native beetle species have become established in Canada, with most species in the Staphylinidae (153 spp.), Curculionidae (107 spp.), Chrysomelidae (56 spp.) and Carabidae (55 spp.). Brunke et al. (2019) estimate that slightly more than 1000 beetle species remain to be reported from Canada, either as new records or undescribed species.

Beetles are important in most natural terrestrial and freshwater ecosystems, have a great effect on agriculture and forestry, and are useful model organisms for many types of science (Bouchard et al. 2017). Because of their greater diversity of species and trophic roles, and their great sensitivity to environmental perturbations, a better understanding beetle biodiversity will enhance our knowledge of the world and provide many practical applications. More information is needed on the habitat affinities of individual species.

We investigated the beetle biodiversity with diverse methods in southern Québec (Canada) over 2006–2012. In the first five years of this study, we explored the spatio-temporal variations of the composition and structure of flying beetle assemblages from a grassland and an adjacent woods, and also the edge effects.

Materials and Methods

Study site. We study beetles at Scotstown (45°32'00" N, 71°17'00" W, about 370 m a.s.l.), 10 km at north of Mont Mégantic, in southern Québec. This site, about 350 m by 60 m, includes a grasssland (pasture for horses during many years and abandonned since 2004) in its upper part (40%), and a

Table 1. Number of individuals and species for six trophic groups of beetles over 2006–2010

		Individuals		Species	
Trophic Groups	**Year**	**N**	**%**	**n**	**%**
Zoophagous	2006	1879	26.4	190	39.6
	2007	1911	24.9	156	34.8
	2008	1324	20.4	155	36.4
	2009	1064	20.6	135	37.0
	2010	1133	13.8	168	40.4
Phytophagous	2006	3951	55.6	167	34.8
	2007	4540	59.3	167	37.3
	2008	4020	61.8	154	36.2
	2009	3397	65.7	129	35.3
	2010	6098	74.5	133	32.0
Saprophagous	2006	791	11.1	53	11.0
	2007	912	11.9	61	13.6
	2008	935	14.4	54	12.7
	2009	532	10.3	44	12.1
	2010	610	7.5	54	13.0
Fungivorous	2006	428	6.0	52	10.8
	2007	260	3.4	52	11.6
	2008	170	2.6	44	10.3
	2009	105	2.0	36	9.9
	2010	182	2.2	48	11.5
Xylophagous	2006	12	0.2	10	2.1
	2007	14	0.2	5	1.1
	2008	17	0.3	13	3.1
	2009	15	0.3	10	2.7
	2010	9	0.1	7	1.7
Others (non-feeding, unknown)	2006	46	0.6	8	1.7
	2007	25	0.3	7	1.6
	2008	39	0.6	6	1.4
	2009	58	1.1	11	3.0
	2010	152	1.9	6	1.4

mixed woods dominated by alders (*Alnus* sp.) in its lower part (60%). A ditch, generally partially or totally shaded by shrubs and trees, is parallel to the grassland and the woods.

Five-year study. During the entire snow-free season (April or May to October), in 2006–2010, we used flight interception traps (FIT) of the type "window trap", with a transparent acrylic sheet (1.2 m height, 0.6 m width), white pan traps on both sides and the use of a germicid detergent. A FIT at the soil level was located at the woods edge, in the grassland at 50 m from the edge, in the woods at 50 m from the edge, and also near the ditch in its lower part (at about 150 m from the River au Saumon).

Trophic groups. Alike Didham et al. (1998), and Grimbacher and Stork (2007), we assigned beetles to six trophic groups: 1) zoophagous (predators and parasitoids), 2) phytophagous (herbivors; feeders of algae, bryophytes, pollen or seeds), 3) fungivors, 4) saprohagous (including dung beetles and detritivors), 5) xylophagous (including xylomycetophagous), and 6) others (non-feeding or unknown). Where only one feeding biology was known for a family, all species were assigned to that trophic group. In other cases, where multiple feeding biologies were known to occur, species were assigned on an individual basis using published details of the feeding biology of the genus or of related genera. The feeding behavior of carabids as a group is difficult to characterize; of the approximately 40 000 described species of

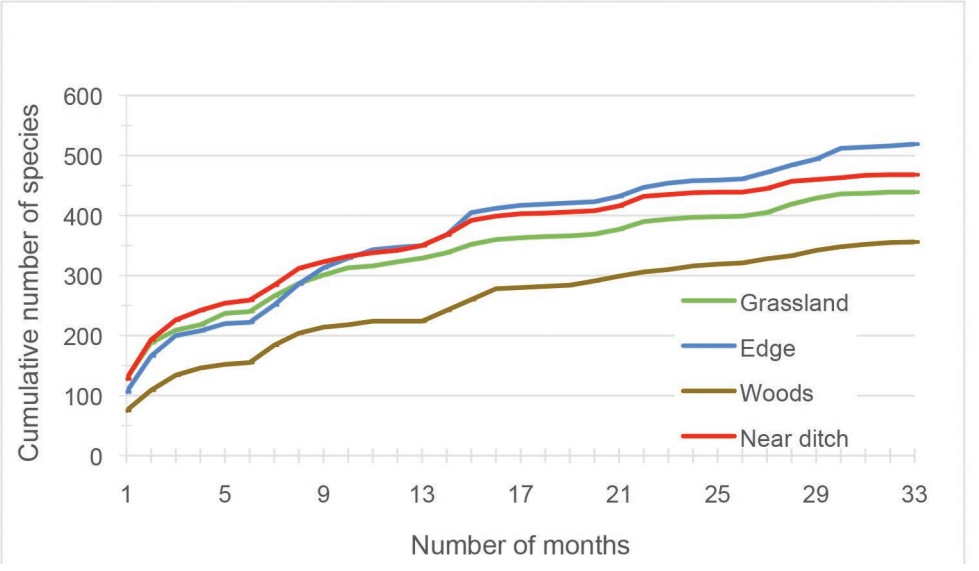

Figure 1. Cumulative number of beetle species for each trap over 33 sampling months in 2006–2010

Carabidae, feeding habits are only described for 2.6% of species; carabids range from nearly complete carnivory (as in most Carabini) to nearly complete herbivory (as in some Harpalini, Zabriini) (Lundgren 2009). Klimaszewski (2000) has presented a synthesis on the feeding habits of rove beetles; most Staphylinidae are generalist predators on other arthropods, but some are specialized to utilize other food resources (as mushrooms, pollen, algae, decomposing organic material). In northern Nearctic forests, about 80% of rove beetle species are predators (Pohl et al. 2008).

Results

Abundance and species richness. Over 2006-2010, we collected with FIT a total of 34 629 individuals of 848 Coleoptera species belonging to 60 families. Seven families were more abundant: Staphylinidae (9743 individuals; 276 species), Nitidulidae (6209; 22), Chrysomelidae (5221; 65), Carabidae (2607; 94), Elateridae (2564; 33), Curculionidae (2425; 83) and Hydrohilidae (1894; 23); these families represented 88.5% of individuals and 70.3% of collected species. We observed the presence of 40 Holarctic species (19.1% of individuals) and 126 adventive species (19.3% of individuals). In FIT, we caught mainly phytophagous (about 35% of species) and zoophagous beetles (near 40%) (Table 1); the relative variations for six trophic groups from year to year were of small amplitudes.

We collected a total of 7107 individuals of 482 species in 2006, 7662 individuals of 446 species in 2007, 6505 individuals of 425 species in 2008, 5171 individuals of 366 species in 2009, and 8184 individuals of 416 species in 2010. The number of individuals by species over the five years ranged from 1 to 5498 adults. The majority of species appeared as singletons (276 species, 32.5%) or in small numbers (2–9 adults; 345 species, 40.7%). Some species in low numbers in window traps may be collected in large numbers with other methods.

Over 2006–2010, we collected a total of 9214 individuals of 439 species in the grassland, 7503 individuals of 519 species at the woods edge, 5943 individuals of 356 species in the woods, and 11969 individuals of 468 species near the ditch. We present the curve of the cumulative number of beetle species collected by each trap over 33 months in 2006–2010 (Fig. 1). At the end of the first sampling year (2006), we have recorded only 240 species in the grassland, 222 species at the woods edge, 155 species in the woods, and 259 species near the ditch; thereafter, over 2007–2010, we observed near 300 other species at the woods edge, and near 200 additional species in the three other window traps. After five years of trap operation, the curve of the cumulative number of species for each trap may indicate almost the final total of species in the surroundings of a trap. The most frequent species were *Longitarsus luridus* (Scopoli) and *Atomaria lewisi* Reitter

Table 2. Total catches of dominant and subdominant beetle species in each trap over 2006–2010, and variations of annual percentages

Species	FAM.[a]	N	%	MIN.%–MAX.%
	Grassland			
Meligethes nigrescens Stephens	NIT	3156	**34.3**	10.3 – 59.6
Longitarsus luridus (Scopoli)	CHR	659	**7.2**	1.7 – 23.7
Hydrothassa vittata (Olivier)	CHR	445	4.8	1.7 – 8.2
Dalopius pallidus Brown	ELA	308	3.3	1.3 – 6.7
Acidota subcarinata Erichson	STA	209	2.3	1.4 – 3.8
Bradycellus nigrinus (Dejean)	CAR	191	2.1	1.8 – 2.4
	Woods edge			
Isochnus rufipes (LeConte)	CUR	1193	**15.9**	8.8 – 34.0
Eusphalerum pothos (Mannerheim)	STA	1061	**14.1**	1.1 – 35.2
Bradycellus nigrinus (Dejean)	CAR	418	**5.6**	2.9 – 7.2
Cercyon assecla Smetana	HYD	399	**5.3**	3.0 – 8.1
Longitarsus luridus (Scopoli)	CHR	385	**5.1**	0.2 – 19.7
Acidota subcarinata Erichson	STA	234	3.1	1.2 – 5.3
Dalopius vagus (Brown)	ELA	200	2.7	1.3 – 5.2
Meligethes nigrescens Stephens	NIT	166	2.2	0.7 – 3.1
Bradycellus semipubescens Lindroth	CAR	165	2.2	1.5 – 3.4
	Woods			
Eusphalerum pothos (Mannerheim)	STA	1184	**31.7**	8.6 – 55.3
Cercyon assecla Smetana	HYD	594	**10.0**	5.0 – 20.2
Bradycellus nigrinus (Dejean)	CAR	239	4.0	1.9 – 7.6
Tachinus luridus Erichson	STA	224	3.8	1.4 – 7.3
Bisnius blandus (Gravenhorst)	STA	189	3.2	2.7 – 4.4
Catops basilaris Say	LEI	157	2.6	1.4 – 4.4
Acidota subcarinata Erichson	STA	155	2.6	0.2 – 7.9
Bradycellus semipubescens Lindroth	CAR	149	2.5	0.8 – 4.8
Dalopius vagus (Brown)	ELA	146	2.5	1.5 – 4.2
Isochnus rufipes (LeConte)	CUR	128	2.2	0.1 – 3.3
	Near ditch			
Longitarsus luridus (Scopoli)	CHR	2561	**21.4**	4.5 – 37.0
Meligethes nigrescens Stephens	NIT	2139	**17.9**	6.0 – 37.0
Acidota subcarinata Erichson	STA	1435	**12.0**	8.2 – 18.3
Ctenicera tarsalis (Melsheimer)	ELA	475	4.0	3.0 – 6.1
Cercyon assecla Smetana	HYD	455	3.8	0.6 – 11.5
Dalopius pallidus Brown	ELA	395	3.3	2.0 – 5.8
Dalopius vagus (Brown)	ELA	247	2.1	1.3 – 3.2

[a] Families : CAR Carabidae; CHR Chrysomelidae; CUR Curculionidae; ELA: Elateridae; HYD Hydrophilidae; LEI Leiodidae; NIT Nitidulidae; STA Staphylinidae

/ *A. fuscata* Schönher (during 30 months) in the grassland, and *Bradycellus nigrinus* (Dejean) (during 30 months) at the woods edge; however, between 39 and 47% of species from a trap were collected in one month only.

Dominant and subdominant species. A dominant species represented at least 5% of catches in a trap, and, a subdominant species, between 2 and 5%. Seven species were dominant in at least one trap over 2006–2010 (Table 2): *Acidota subcarinata* Erichson near the ditch, *B. nigrinus* at the woods edge, *Cercyon assecla* Smetana at the woods edge and in the woods, *Eusphalerum pothos* (Mannerheim) at the woods edge and in the woods, *Isochnus rufipes* (LeConte) at the woods edge, *L. luridus* in the grassland, at the woods edge and mainly near the ditch, and *Meligethes nigrescens* Stephens in the grassland and near the ditch. In a trap, some dominant and subdominant species showed considerable fluctuation in percentage from year to year; for examples, between 8.6 and 55.3% for *E. pothos* in the woods, between 4.5 and 37.0% for *L. luridus* near the ditch, and between 10.3 and 59.6% for *M. nigrescens* in the grassland.

Table 3. Total catches, habitat preferences, biogeography, trophic groups, activity months and female ratio of the most abundant species over 2006-2010

Family and species	N	Hab.[a]	Biog.[b]	Gr.[c]	Activity months[d] A M J J A S O	Fem. (%)
Carabidae						
Bradycellus lugubris (LeConte)	128	G		P	A **M** J	62
Bradycellus neglectus (LeConte)	116	G		P	A **M** J A S O	56
Bradycellus nigrinus (Dejean)	1067	G		P	**A M** J J A S O	55
Bradycellus semipubescens Lindroth	507	G		P	**A M** J J A S	56
Chrysomelidae						
Altica corni Woods	124	F		P	A **M J** J A S O	69
Hydrothassa vittata (Olivier)	569	O	H	P	A **M** J J A S O	na
Longitarsus luridus (Scopoli)	3660	O	A	P	A M J J A **S O**	44
Coccinellidae						
Harmonia axyridis (Pallas)	152	O	A	Z	A S **O**	59
Cryptophagidae						
Atomaria ephippiata Zimmernann	281	O		F	M **J** J A S	60
Atomaria lewisi Reitter / *A. fuscata* Sch.	264	O	A/H	F	A **M J** J A S O	na
Curculionidae						
Eutrichapion cyanitinctum (Fall)	252	O		P	A M J J A **S O**	67
Isochnus rufipes (LeConte)	1363	F		P	A M **J J** A **S** O	65
Phyllobius oblongus (L.)	157	G	A	P	M **J J**	na
Elateridae						
Ctenicera tarsalis (Melsheimer)	566	O		P	A **M** J	20
Dalopius pallidus Brown	740	O		P	A **M J** J A	29
Dalopius vagus (Brown)	721	G		P	M **J J** A S O	35
Hypnoidus abbreviatus (Say)	143	O		P	A **M** J J	59
Hydrophilidae						
Cercyon assecla Smetana	1534	G		S	A M J J **A S** O	59
Lampyridae						
Ellychnia corrusca (L.)	309	G		Z	A **M J** J A S O	37
Leiodidae						
Catops basilaris Say	236	F		S	M J **J** A S	48
Sciodrepoides teminans (LeConte)	137	G		S	M J **J** A	60
Mordellidae						
Mordellina sp. S	242	O		P	J **J A** S	49
Nitidulidae						
Carpophilus brachypterus (Say)	138	O		S	A **M J** J A	54
Conotelus obscurus Erichson	168	O		P	J J **A S** O	55
Glischrochilus quadrisignatus (Say)	259	G		S	A **M J** J S	na
Meligethes nigrescens Stephens	5498	O	H	P	A **M J** J A S O	9
Pedilidae						
Pedilus canaliculatus (LeConte)	226	O		P	**M J** J	38
Scirtidae						
Cyphon variabilis (Thunberg)	242	G		?	A **M** J J A S O	64
Silphidae						
Necrophila americana (L.)	189	O		S	M **J J** A	33
Staphylinidae						
Acidota subcarinata Erichson	2033	G		Z	M J **S O**	11
Acrotona sp. S4 + *Mocyta luteola* (Er.)	109	O		Z	A **M** J J A S	na
Amischa analis (Gravenhorst)	242	O	A	Z	A **M J** J A S O	100
Anotylus rugosus (Fabricius)	113	O	A	S	A **M** J J A	66
Atheta crenuliventris Bernhauer	247	O		Z	M J **J A** S O	40
Atheta districta Casey	157	F		Z	M J **J A** S O	51
Bisnius blandus (Gravenhorst)	229	F		Z	A M J **J A** S	52
Carpelimus sp. S02	100	?		S	A **M** J J A S O	na
Eusphalerum pothos (Mannerheim)	3159	F		P	**M J** J A	53
Gabrius subnigritulus (Reitter)	101	O	A	Z	A **M** J J A S O	72
Mocyta fungi (Gravenhorst)	244	O	A	Z	A **M** J J A S O	na
Ontholestes cingulatus (Gravenhorst)	175	O		Z	A M **J J** A S	46
Oxytelus laqueatus (Marsham)	109	F	A	S	M **J** J **A** S O	55
Philhygra clemens Casey	101	O		Z	A **M J** J A S O	na
Philonthus carbonarius (Gravenhorst)	119	O	A	Z	A **M** J **J** A S O	54
Philonthus cyanipennis (Fabricius)	114	F	H	Z	M **J J** A	57
Quedius curtipennis Bernhauer	121	O	A	Z	A **S** O	55
Tachinus luridus Erichson	326	F		Z	M J **J** A S	54
Tachyporus dispar (Paykull)	150	O	A	Z	A **M J** J A S O	58

[a] Habitat preferences: F forest; G habitat generalist; O open site; ? indetermined
[b] Biogeography: A adventive species; H Holarctic species
[c] Trophic groups: F fungivorous; P phytophagous; S saprophagous; Z zoophagous; ? unknown
[d] At least 25% of catches during months in bold

On the basis of the species richness and idendity of the dominant and subdominant species, the composition of the beetle assemblage at the woods edge was intermediary between the assemblages in the grassland and in the woods; whereas the composition of the beetle assemblages in the grassland and near the ditch were more similar.

The most abundant species. We collected at least 100 adults for 48 species, representing 80.7% of beetles in the four traps over 2006–2010 (Table 3), including four major species: *M. nigrescens* (15.9%), *L. luridus* (10.6%), *E. pothos* (9.1%), and *A. subcarinata* (5.9%). We believe that nine species were forest species (predominantly occurring in forests), 12 were habitat generalists, and 26 species were generally in open sites and / or in boundary (woods edge or near the ditch). Among the 48 most abundant species, 15 taxa are Holarctic or adventive, including three very abundant phytophagous species (*Hydrothassa vittata* (Olivier), *L. luridus* and *M. nigrescens*), and an adventive species (*Quedius curtipennis* Bernhauer) recently recorded in southern Québec. These species included two fungivorous taxa, 19 phytophagous species, nine saprophagous species, 17 zoophagous species and one species of unknown trophic group. We observed a wing polymorphism in *L. luridus* (Chrysomelidae Alticini): 5.5% of individuals were macropterous; whereas adults of 47 other abundant species were all macropterous. Two species, *E. pothos* and *M. nigrescens*, were mainly active in May and June; however, adults of *A. subcarinata* and *L. luridus* were collected mainly in September and October. We observed generally the flight of females and males in similar numbers, but we caught mainly males (~90%) of *A. subcarinata* and *M. nigrescens* (Table 3).

Discussion

Owen (1993) used a flight interception trap in studying the beetle fauna of a Surrey (UK) woods over a three year period. He collected a total of 10581 individuals belonging at 499 species (average of 320 species / year). The number of individual by species over the three years ranged from 1 to 841. The majority of species appeared as singletons (132 species) or in small numbers (2–10 individuals, 238 species). Many species were trapped in one year but were not caught in either of the two other years. The extrapolation of the cumulative total of species at the end of each year of this survey indicates that the final total achieved with the trap (after many years of operation) would be in the range of 580 species. Some species showed considerable fluctuation in number; very few showed an uniform abundance over the three years. More beetles and species occurred in the warmer months of the year; 82% of the total catches and 61% of species were trapped in April-September; certain species occurred over relatively short periods whereas others had an extended season.

In a previous study, we investigated the flight of beetles in a raspberry agro-ecosystem at Johnville (about 50 km from Scotstown, southern Québec) over 1987–1989 (Levesque and Levesque 1992, 1993a, 1993b, 1994a, 1994b, 1995a, 1995b, 1995c, 1996, 1997, 1998). We used four FIT, three near raspberry plants (two in open sites, one at a woods edge), and one in an adjacent pine woods. The species composition of beetle assemblages was quite similar over the years in each trap, except at the woods edge because of variations in the relative abundance of species flying either in open sites or in wooded sites. Among the 42 most abundant species (excluding Aleocharinae) in FIT at Scotstown, at least 27 species were also collected at Johnville. Our observations for these 27 species on the phenology patterns, female ratio, wing polymorphism and habitat preferences were quite similar over 1987–1989 and 2006–2010. The total number of *L. luridus* catches from Johnville was increased by a factor of 6.5 between 1987 and 1989, this difference mainly associated with the new generation adult activity during the autumn (Levesque and Levesque 1998). However, we did not observe important differences for *E. pothos* and *M. nigrescens* captures from year to year at Johnville (Levesque and Levesque 1992 and 1996).

Generally, our observations on beetles from Scotstown were quite similar at these of Owen (1993) and Levesque and Levesque (1992–1998). Species-level responses driven probably by differences in behavior, dispersal ability, ecological interactions, abundance of ephemeral habitats, microclimate, or spatial heterogeneity in food quality and quantity (Maguire et al. 2014).

Community composition of Coleoptera varied significantly by trap height and time in the north-temperate forests (Barsulo and Nakamura 2011, Hardersen et al. 2014, Irmler 1998, Maguire et al. 2014, Normann et al. 2016), and also in agricultural landscapes (Boiteau et al. 1999, 2000a, 2000b, Stein 1972). Highest abundance and species richness were observed in the lowest stratum at all sites, where phytophagous and predators were more abundant.

One of the factors associated with FIT data is that many species are wide-ranging "tourists" that are sometimes found in habitats where they do not reproducte or develop (Zeran et al. 2006). The combined influence

of structural and compositional habitat heterogeneity at stand (within a 11.3 m radius) and landscape scales (within 400 or 800 m radius) best explained richness patterns in flying beetles in a matrix of old-growth boreal forest in Québec (Janssen et al. 2009).

In last years, some researches have focused on the biodiversity of beetles from many sites during one or two years. However, we believe that this type of research could explore more often variations on long time, particularly in the study on influences of climatic changes, because 1) the difficulties to estimate the real species richness of flying Coleoptera in a site, even after a five-year sampling, and 2) the possible considerable fluctuation of annual percentages for the most abundant species in a flight interception trap installed in an undisturbed site.

Acknowledgments

We are grateful to P. Bouchard, Y. Bousquet, A. Davies, S. Laplante, late L. LeSage, A. Smetana and A. Zmudzinska (National Identification Service (Entomology), Agriculture and Agri-Food, Ottawa, Canada), and J. Klimaszewski (Natural Resources Canada, Canadian Forest Service, Québec, Canada) for taxonomic help. We thank the reviewers.

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Acroneuria lycorias (Boreal Stonefly, Plecoptera: Perlidae) Emergence Behaviors Discovered in *Pinus strobus* Canopy

Hannah Hoff[1], Jonathan G. Martin[1], Patrick J. Liesch[2], and Erik R. Olson[1,*]

[1] Northland College 1411 Ellis Ave, Ashland, Wisconsin, USA

[2] University of Wisconsin – Madison, Insect Diagnostic Lab, 1630 Linden Drive, Madison, Wisconsin, USA

*Corresponding author: (email: eolson@northland.edu)

Abstract

Species of Plecoptera, or stoneflies, are known to use vertical emergence supports, and researchers believe many species of Plecoptera exploit arboreal habitats during emergence. However, the exact nature of these arboreal behaviors has largely remained a mystery. While exploring the habitat potential of *Pinus strobus* (L.) (Eastern White Pine) canopies in northern Wisconsin we observed *Acroneuria lycorias* (Newman) (Boreal Stonefly, Plecoptera: Perlidae) exuviae at heights as high as 12 m (observations at 6.6, 9, 9.5, and 12 m). Most *A. lycorias* exuviae appeared to have a strong preference for emergence sites at the underside or base of branches similar to some Odonate species. We also observed *A. lycorias,* adults climbing upwards along the main stem, post-emergence, to heights up to 22 m. To our knowledge, these heights represent the greatest heights ever documented for *A. lycorias* adults and exuviae, or any Plecopteran species. While other researchers have speculated that *A. lycorias* uses arboreal habitats during emergence, these behaviors were considered almost impossible to describe. Our observations provide us with new insights into Plecopteran emergence behaviors, especially for this species. We propose three alternative hypotheses that may explain these unique emergence behaviors.

Keywords: arboreal habitat, emergence, Plecoptera, stonefly

Species of Plecoptera, or stoneflies, are known to use vertical emergence supports, and researchers believe many species of Plecoptera exploit arboreal habitats during emergence. However, the exact nature of these arboreal behaviors has largely remained a mystery. In 2014, we began exploring the habitat potential of *Pinus strobus* (L.) (Eastern White Pine) canopies in northern Wisconsin (Laughlin et al. 2018). While climbing a large and old (>85 cm diameter at breast height, >100 years) *P. strobus* research tree on 6 June 2018, we observed *Acroneuria lycorias* (Newman) (Boreal Stonefly) exuviae and adults at various heights in the canopy (Fig. 1). We observed multiple *A. lycorias* exuviae at heights as high as 12 m (observations at 6.6, 9, 9.5, and 12 m). Most *A. lycorias* exuviae appeared to have a strong preference for emergence sites at the underside or base of branches. Laughlin et al. (2018) also observed an apparent selection for the underside or base of branches during emergence for multiple species of Odonata. We also observed multiple adult *A. lycorias* climbing upwards along the main stem and branches above the exuviae at heights up to 22 m. To our knowledge, these heights represent the greatest heights ever documented for *A. lycorias* adults and exuviae, and any other Plecopteran species.

All exuviae and adults were observed on the southwest side of the study tree, which faced the nearby river. This tree was located approximately 10 m from the bank of the White River, a stream surrounded by tall clay banks in Ashland, Wisconsin, USA. The shore that surrounded this tree is forested with a number of old-growth and second-growth trees that have undergone minimal management under ownership of Northland College (Ashland, WI, USA) since region-wide harvests from 1890-1900. Shortly after these observations, this particular research tree was lost during a flood and no additional observations were made. Exploration of another *P. strobus* tree further from the river's edge and during the month of August yielded no additional observations.

Exuviae (n = 5) and adults (n = 1; female) were collected and identified using the keys in Hitchcock (1974), Stark and Gaufin (1976), and Stewart and Stark (2008). Specimens from the Hilsenhoff Aquatic Insect Collection at the Wisconsin Insect Research Collection (Madison, WI, USA) were also examined to verify the species. In northern

Figure 1. Adult *Acroneuria lycorias* observed climbing along main stem at 16 m. Exuviae were observed up to 12 m and adults were observed climbing along the main stem at heights up to 22 m.

Wisconsin, three *Acroneuria* species can be encountered: *A. abnormis* (Newman) (Common Stone), *A. internata* (Walker) (Lobed Stone), and *A. lycorias* (Dewalt et al. 2019). Of these, nymphs and exuviae can be readily identified using the taxonomic keys in Hitchcock (1974). Adult female *A. lycorias* can be separated from other *Acroneuria* spp. by the remnants of subanal gills, a darkened ocellar triangle, colored bands on the abdominal segments, and the shape of the subgenital plate. The shriveled anal gills can help identify adult male *A. lycorias* specimens, although examination of the paraprocts and the genitalia are required to identify some species in this group.

These observations provide us with new insights into Plecopteran species emergence behavior, which is poorly understood, especially for this species (Narf and Hilsenhoff 1974, Poulton and Stewart 1988, Sheldon 1999). Mature Plecopteran nymphs are known to crawl out of streams and cold lakes where eggs are laid, and climb vertical surfaces such as logs or the base of trees as emergence supports (Hynes 1976). There, they transform to the adult stage, leaving exuviae at the emergence site. In Wisconsin, adults are known to emerge during a two-week period in early spring while water temperatures remain below 10 °C (Krzysztof and Szczytko 1984) and mate while resting on a horizontal substrate (Peckarsky 1979). Most species appear to select for emergence sites near the ground (Hynes 1976). Thus, our observations of *A. lycorias* exuviae at heights up to 12 m substantially expands the known range of heights for Plecopteran emergence. Laughlin et al. (2018) also documented that certain species of odonates use emergence sites at great heights in *P. strobus* canopies. Additionally, our observations of post-emergence behavior by adult *A. lycorias* (i.e., climbing up the stem following emergence to heights exceeding 22 m) is indicative of a life cycle-related behavior that has been previously undocumented. Narf and Hilsenhoff (1974) speculated that *A. lycorias* adults inhabit tree canopies in Wisconsin, but they dismissed collection of specimens in the canopy as "almost impossible" (p.124). Szczytko and Kondratieff (2015) also acknowledged the difficulty of collecting adult Plecopterans. Our observations indicate that *A. lycorias* may have a two-step process of canopy utilization where nymphs climb to heights well above the forest floor in preparation for emergence. Post-emergence, *A. lycorias* adults then climb up the stem of the structure to the upper canopy.

Why *A. lycorias* uses the canopy for these life-cycle related behaviors, remains

an open question. Adult *Acroneuria* have a short lifespan and are not known to feed (Peckarsky 1979), so utilization of the canopy for the consumption of organic material is unlikely. This life history trait (i.e., upward movement of adults following emergence) may be beneficial for maintaining genetic diversity by facilitating long-distance dispersal, for reducing competition between species through spatially-constrained niche partitioning, or for hastening growth and life stage development via exploitation of warmer and drier microclimates associated with the canopy.

As Plecoptera are considered weak-flying or non-flying insects (Marden and Kramer 1994), climbing to great heights may facilitate dispersal. Plecopteran dispersal is difficult to study directly and "dispersal events that are biologically important may remain undetected" (Winterbourn et al. 2007, p. 1). Adult Plecoptera numbers tend to decline with increasing distance from stream, with 90% of adults caught within 11 m of a stream channel, suggesting that only a limited number of individuals are likely to disperse between streams (Briers et al. 2002). In few cases, adults have been observed > 40 m away from their natal streams (Briers et al. 2004); these few long-distance dispersers may play a significant role in maintaining genetic diversity (Winterbourn 2005). Limited by poor flight, upward movement of adult Plecoptera to the upper canopy may allow greater dispersal distances.

Alternatively, species of Plecoptera exhibit temporal displacement of life cycles to reduce interbreeding and competition (Peckarsky 1979, Dewalt and Stewart 1995). *Acroneuria lycorias* may co-occur with species such as *A. abnormis*, and in such cases, *A. lycorias* nymphs have been observed emerging slightly earlier than *A. abnormis* individuals (Harper and Pilon 1970). This temporal segregation of emergence may prevent interbreeding and reduce competition for food resources and space for drumming and courtship behavior (Peckarsky 1979). The climbing behavior we observed may provide a secondary mechanism of reproductive isolation and reduce competition for drumming sites, allowing multiple species to coexist in close proximity to their natal stream through separation along a vertical gradient.

Finally, the use of canopies may also be beneficial for hastening growth and life stage development which can be linked to drier and warmer conditions (Ernst and Stewart 1985, Poulton and Stewart 1988). Sites in the canopy may be warmer and drier due to increased solar exposure and greater air flow relative to sites near the ground.

Plecoptera are intolerant of environmental stressors and have been speculated to be the insect order most threatened by human encroachment (Hynes 1993). Thus, it is important to understand the distribution and diversity of Plecoptera for the maintenance and restoration of aquatic biodiversity. Our research draws additional ecological connections between riparian forest canopies and aquatic life that can have important conservation implications; best management practices for timber harvest often include protection of riparian corridors. Our understanding of the role riparian forest canopies may have in the maintenance of aquatic systems is still expanding, and our work further supports efforts to conserve riparian corridors. With ongoing research and monitoring, we can better understand the ecological importance of forest canopies and forested riparian corridors to Plecoptera and other aquatic species.

Acknowledgments

This project was made possible through a grant from the John C. Bock Foundation. We acknowledge the foresight of Madison Laughlin in making this project a reality. We thank two anonymous reviewers for their thoughtful feedback regarding an earlier version of this manuscript.

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New State Records for the Cicada Parasite Beetle *Sandalus petrophya* Knoch (Coleoptera: Rhipiceridae) in Nebraska and Iowa

Edwin L. Freese
33493 "S" Avenue, Adel, Iowa 50003 (e-mail: freeseedwin@yahoo.com)

Abstract

New state records are presented for *Sandalus petrophya* Knoch (Coleoptera: Rhipiceridae) specimens from Nebraska and Iowa along with the currently known distribution of this beetle species.

The cicada parasite beetle also known as the cedar beetle *Sandalus petrophya* Knoch (Coleoptera: Rhipiceridae), is reported from Nebraska for the first time, with three individuals collected near Bennet, Lancaster Co., Nebraska, 31 July 2018, flying around cedars, specimens collected by M.J. Paulsen (Paulsen, pers. comm., July 2018); the two male specimens were 11.5 mm long and the female specimen was 13.5 mm long [photo posted on internet at http://bugguide.net/node/view/1566554]. Four more specimens (3 males and one female) were collected at the same location at one juniper tree, 1 August 2018, with no further specimens the following days (Paulsen, pers. comm., August, October 2018); the collecting location is a quarter section of rolling pasture being invaded by cedar trees (Paulsen, pers. comm., October 2018). Kyle Schnepp in a return e-mail to M.J. Paulsen confirmed the new state record (Paulsen, pers. comm., August 2018).

The first three specimens known from Iowa were sorted from a Lindgren funnel trap sample collected near Adel, Dallas Co., Iowa, 29 July to 13 August 2018, oak-hickory woodland with elm, black cherry, hackberry, honey locust, and cedar trees [area was a mowed wooded pasture until the mid-1980s], by the author having just returned from a two-week vacation trip. The two male specimens were 11 mm long and the female specimen was 14 mm long. Kyle Schnepp indicated he had not seen any specimens of this species from Iowa (Schnepp, pers. comm., September 2018). A fourth specimen was later located in the Iowa State University insect collection (ISIC), Ames: Des Moines, Polk Co., Iowa, 12 August 1942, W. W. Darlington [female, 16 mm long].

Schnepp and Powell (2018) published the most recent article covering the genus *Sandalus* Knoch, 1801, which included a key to the three species of the eastern United States. The cedar beetle *S. petrophya* was previously known from the following states: AL, DC, FL, GA, IL, IN, KY, LA, MD, MO, NC, NJ, NY, OH, PA, TN, VA, and WV (Evans & Steury 2012).

Acknowledgments

I thank Matt J. Paulsen, University of Nebraska State Museum, Lincoln, for his e-mail bringing this species to my attention while I was away on a two-week vacation and to Kyle E. Schnepp, Florida State Collection of Arthropods, Gainesville, for confirming the two new state records. Thank you also to Gregory W. Courtney, Iowa State University, Ames, for access to the insect collection. Also to my wife Janet E. Freese for her personal knowledge of the family farm and wooded area from which the specimens were trapped.

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The Great Lakes Entomologist
Published by the Michigan Entomological Society

Volume 52 Nos. 1 & 2

ISSN 0090-0222

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Cover photo
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